BIOGEOGRAPHY OF BRACONID PARASITOIDS OF THE CARIBBEAN FRUIT FLY, *ANASTREPHA SUSPENSA* (LOEW) (DIPTERA: TEPHRITIDAE), IN FLORIDA

By

AVRAHAM EITAM

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Abstract of Dissertation Presented to the Graduate School
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BIOGEOGRAPHY OF BRACONID PARASITOIDS OF THE CARIBBEAN FRUIT FLY, *ANASTREPHA SUSPENSA* (LOEW) (DIPTERA: TEPHRITIDAE), IN FLORIDA

By

Avraham Eitam

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Host fruits of the Caribbean fruit fly, including loquat, Surinam cherry, Cattley guava and common guava, were collected throughout central and southern Florida. Three species of braconid parasitoids were recovered. *Diachasmimorpha longicaudata* (Ashmead) was limited mostly to southern Florida, reaching higher latitudes along both coasts. *Doryctobracon areolatus* (Szepligeti) was common at most interior locations, but absent or rare along the coasts. Distribution of these two species overlapped only within a limited region, and only at LaBelle (Hendry Co.) did they commonly co-occur. *Utetes anastrephae* (Viereck) was widespread, but its abundance was inversely related with that of *D. areolatus*.

Absence of *D. longicaudata* was related with low temperatures, but was best explained by high variability of temperatures. Two hypotheses are proposed to explain the relationship between temperature and *D. longicaudata* distribution: (1) Low temperatures have a direct negative effect; (2) Variable or low temperatures adversely

affect host availability, which in turn has a negative effect on *D. longicaudata*. Evidence supporting each hypothesis is discussed.

Parasitism levels by *D. longicaudata* in loquat and common guava fruits were significantly related with the minimum and mean numbers, respectively, of Caribbean fruit flies captured in McPhail traps. Similarly, parasitism by *U. anastrephae* in loquat and Surinam cherry fruits was related with minimum fly numbers.

Parasitism levels of all species combined in loquat and Surinam cherry fruits was significantly related with densities of common guava trees. Parasitism by *U. anastrephae* in Cattley guava fruits was related with densities of Surinam cherry plants.

The apparent disappearance of *D. areolatus* from the southern Atlantic coast, where it was originally released, may be partially due to interspecific competition. Mechanisms proposed that may give *D. longicaudata* a competitive advantage include better ability to locate larvae within fruits, a longer ovipositor allowing greater access to hosts, higher fecundity, and an advantage in competition among larvae.

At LaBelle, parasitism by *D. longicaudata* in spring fruiting loquat and Surinam cherry was positively related with the preceding winter temperatures. A similar relationship was found for *D. areolatus*, but only in loquat fruits. A negative relationship between parasitism by *D. areolatus* and *D. longicaudata* was observed at the peak of the Surinam cherry fruiting season, suggesting that significant competition may occur.

CHAPTER 1
GENERAL INTRODUCTION: THE CARIBBEAN FRUIT FLY AND ITS PARASITOIDS IN FLORIDA

The Caribbean fruit fly, *Anastrepha suspensa* (Loew), became established in Florida in 1965, quickly spreading throughout southern and central Florida (Weems 1966). In Indian River County, *A. suspensa* occurrence was linked primarily with the availability of various host fruits (Nguyen et al. 1992). Flies were collected mainly from loquat (*Eriobotrya japonica* (Thunb.)) during December-April, Surinam cherry (*Eugenia uniflora* L.) during May-June, and Cattley guava (*Psidium cattleianum* Sabine) during July-August, with greatest numbers reported from the latter two fruits. A population increase during one of the survey years in November-December was related to a second crop of Surinam cherry. In Dade County, weekly trap catches appeared to mirror temperature fluctuations (Hennessey 1994). Correlations of fly catches with rain and temperature together were significant for most years. Hennessey (1994) concludes that abiotic environmental factors and host availability interact to affect trapping frequency.

In an effort to control *A. suspensa*, several species of parasitoids were introduced to Florida (Baranowski et al. 1993). The first to be released was *Doryctobracon areolatus* (*Parachasma cereus*) (Szepligeti) (Hymenoptera: Braconidae: Opiine) (Baranowski and Swanson 1970). This is a widespread larval-pupal species, ranging from Mexico to Argentina (Wharton and Marsh 1978). An original stock of 7 males and 17 females from Trinidad was reared through 6-7 generations, and 45 males and 26 females were released

at Homestead in 1969 (Baranowski et al. 1993). Although it was recovered in large numbers the following summer, populations at this site have since declined (Baranowski et al. 1993). Small numbers persisted in the area at least until the occurrence of Hurricane Andrew in 1992 (Sivinski 1991, pers. comm.).

Studies indicate that *D. areolatus* abundance varies among locations in Florida. Sivinski et al. (1996) report it to be the dominant parasitoid in areas west of Lake Okeechobee. However, it was absent from their samples in southeastern Florida. Holler (unpublished data) failed to recover this species in a survey preceding augmentative releases of *Diachasmimorpha longicaudata* (Ashmead) along the central Atlantic coast of the state. However, subsequent intensive fruit sampling during 1993-1994 produced 16 *D. areolatus* from 7 trees (Denise Marshall, pers. comm.).

D. longicaudata, another larval-pupal opiine braconid, was introduced in 1972. This Indo-Philippine species was originally recovered from *Bactrocera* spp. (Clausen 1978). It has been utilized in the biological control of a wide range of tephritid hosts in various regions of the world (see Chapter 2). In contrast to the limited release of *D. areolatus*, *D. longicaudata* was released in large numbers in 21 counties throughout central and southern Florida (Baranowski et al. 1993). Based on reduced fly catches in subsequent years, it appeared to have had a significant impact upon host fly populations (Baranowski et al. 1993).

Two other exotic larval-pupal parasitoids, *Aceratoneuromyia indica* Silvestri (Hymenoptera: Eulophidae) and *Trybiographa daci* Weld (Hymenoptera: Eucoilidae), also were considered established (Baranowski et al. 1993). In addition two larval-pupal braconid parasitoids, *Utetes anastrephae* (Viereck) and *Doryctobracon anastrephilum*

(Marsh), were recovered in small numbers prior to the parasitoid releases. These were considered to have originally existed on *Anastrepha interrupta* Stone in the Florida Keys (Baranowski et al. 1993). Like *D. areolatus*, *U. anastrephae* is a wide ranging species, distributed south to Argentina (Wharton and Marsh 1978).

Sivinski et al. (1998) investigated the temporal dynamics of *D. longicaudata* and *D. areolatus* populations at LaBelle. *D. longicaudata* became more abundant, actually and relative to *D. areolatus*, as the season progressed, in all fruits except calamondin (*Citrus mitis* Blanco). Temperature best explained the fluctuations in relative abundance. However, with the exception of the autumn-winter decline of *D. longicaudata* in calamondin, results could also be explained by "counter-balanced competition" (cf. Zwölfer 1971), where *D. areolatus* is superior to *D. longicaudata* in finding host patches, but inferior at exploiting hosts.

Augmentative releases of adult *D. longicaudata* apparently substantially suppressed *A. suspensa* populations at two locations in Florida (Sivinski et al. 1996). Similar results have been reported with releases of *Diachasmimorpha tryoni* (Cameron) for the suppression of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) in Hawaii and Guatemala (Wong et al. 1991, Sivinski et al. submitted). Inundative releases of *D. longicaudata* were being employed for *A. suspensa* control for several years in the central Atlantic coast region of Florida (Burns et al. 1996).

The objectives of this study were to determine the current distribution patterns and relative abundance of *A. suspensa* parasitoids in Florida, and identify factors affecting this distribution. These determinations could assist in the ongoing biological

control effort, by suggesting which parasitoid species should be employed in augmentative releases in various regions of the state.

The following chapter reviews literature on the distribution of tropical and subtropical tephritid fruit flies and their parasitoids in other regions of the world. Chapter 3 describes the geographic distribution of *A. suspensa* parasitoids in Florida, and the environmental factors associated with this distribution. Chapter 4 investigates temporal and spatial dynamics in an area of co-occurrence of parasitoid species within Florida. Subsequent chapters investigate biological attributes which may influence parasitoid distribution and abundance. Chapter 5 examines effects of temperature on *D. longicaudata* adults and immature stages in the laboratory. Chapter 6 describes life history traits of *D. areolatus* in the laboratory. Chapter 7 investigates the host location behavior of *D. areolatus*.

Generic names of opiine braconids in this text are according to the recent revision by Wharton (1997).

CHAPTER 2
LITERATURE REVIEW: DISTRIBUTION, TEMPERATURE TOLERANCE AND DIAPAUSE OF PESTIFEROUS TEPHRITID FRUIT FLIES AND THIER PARASITOIDS IN TROPICAL AND SUBTROPICAL REGIONS

Distribution and Population Dynamics

A great deal of literature has been published concerning distribution of tephritid fruit flies and their parasitoids in various regions of the world. The two regions most extensively studied in this regard have been Hawaii and tropical America. The objective of this review is to identify factors which may be important in explaining fruit fly and/or parasitoid distribution patterns.

Hawaii

Four species of adventive frugivorous tephritids occur in Hawaii. They are melon fly, *Bactrocera cucurbitae* (Coquillett), arrived in 1895; Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), in 1910; oriental fruit fly, *B. dorsalis* (Hendel), in 1945; and Malaysian fruit fly, *B. latifrons* (Hendel), in 1983 (Vargas et al. 1989).

Shortly after its arrival, *C. capitata* became a serious economic pest on various fruits throughout Hawaii (Back and Pemberton 1918). Subsequent to the arrival of the *B. dorsalis*, *C. capitata* became scarce at lower elevations but remained abundant in upland areas (Bess 1953). It was speculated that *C. capitata* had been competitively displaced by *B. dorsalis*, which was better adapted to the warmer climate of the lowlands (Haramoto

and Bess 1970). In guava fruits, *B. dorsalis* larvae suppressed the development of larvae of the *C. capitata* by an unspecified mechanism (Keiser et al. 1974). Since guava is a major host at low altitudes, this could contribute to the displacement of *C. capitata* in these areas. However, *C. capitata* has not been totally displaced at low elevations. Bess (1953) and Keiser et al. (1974) noted that it remained common in preferred hosts, such as coffee, regardless of elevation. During the winter months of 1966-1968 (when total infestation was low) it outnumbered *B. dorsalis* in guava (Haramoto and Bess 1970). Vargas et al. (1983a) studied *C. capitata* distribution on Kauai. Fly abundance was inversely related with elevation, and also with rainfall. Large numbers emerged from peach, loquat, sandalwood, and coffee. Highest populations were in areas containing scattered strands on feral coffee. In newly planted coffee fields in lowland Kauai, *C. capitata* dominated *B. dorsalis* by the end of each of three seasons (Vargas et al. 1995). The authors suggest that infestation of an earlier stage of fruit ripeness and faster development of *C. capitata* larvae in coffee reduce competitive interactions with *B. dorsalis* larvae. Furthermore, they suggest that absence of large overstory trees and a scarcity of alternate hosts may limit *B. dorsalis* abundance in monoculture coffee fields. In studies on Oahu, *C. capitata* was found to occur in larger numbers than *B. dorsalis* in feral coffee, but was less common on other hosts (Harris and Lee 1986, 1987). The abundance of coffee berries and distribution of other fruits apparently influenced fluctuations in *C. capitata* populations. Rainfall had an indirect effect on *C. capitata* dynamics by inducing coffee fruiting (Harris and Lee 1986). In the urban areas of Oahu, there was apparently a more direct effect of rainfall. Medflies were more common in dry,

leeward areas, although the same host fruits were grown there as in wet, windward areas (Harris and Lee 1987).

Population cycles of *B. dorsalis* have been associated with fruiting of common and strawberry guava (Newell and Haramoto 1968, Vargas et al. 1983b). Although abundance is negatively related with elevation on Kauai, it appears that the factor limiting distribution at high elevations is the relative scarcity of hosts (Vargas et al. 1983b). Similarly, high numbers of *B. dorsalis* in wet windward areas vs. dry leeward areas, and outside vs. inside production areas, corresponds with concentrations of wild guava (Vargas et al. 1989, 1990).

The major hosts of *B. cucurbitae* in Hawaii include tomato and various species of wild and cultivated cucurbits (Harris et al. 1986). Fly abundance on Kauai is negatively related with elevation and rainfall. These relationships may be explained by host plant distribution: hosts are not found above 300 m, and grow better in drier areas (Harris et al. 1986). On Molokai, fly distribution is strongly related to that of the feral host bittermelon (Harris and Lee 1989). Similarly, abundance of *B. cucurbitae* in dry leeward areas vs. wet windward areas on Kauai is related to the distribution of bittermelon and spiny cucumber (Vargas et al. 1989). More *B. cucurbitae* were captured inside production areas, again related to abundance of host plants (Vargas et al. 1989, 1990).

B. latifrons develops on a variety of solanaceous and cucurbitaceous plants (Liquido et al. 1994). Although *B. cucurbitae* is the primary fruit fly on most species in these families, *B. latifrons* appears to outcompete other fruit fly species on several host plants that inhabit disturbed, abandoned fields and less managed ranch lands (Liquido et

al. 1994). Populations are apparently affected by both temperature and rainfall. Liquido et al. (1994) suggest that high rainfall excludes this fly from the windward side of Hawaii.

Following the arrival of *C. capitata*, a project was undertaken to introduce fruit fly parasitoids to Hawaii. F. Silvestri (during 1912-1913) and D.T. Fullaway and J.C. Bridwell (in 1914) released several species, 5 of which became established: the opiine braconids *Diachasmimorpha tryoni* (Cameron), *Opius humilus* Silvestri, and *Diachasmimorpha (Biosteres) fullawayi* (Silvestri), the eulophid *Tetrastichus giffardianus* Silvestri, and the chacidid pupal parasitoid *Dirhinus giffardii* Silvestri (Clausen et al. 1965, Gilstrap and Hart, 1987). All species were from Africa, with the exception of *D. tryoni* from Australia.

Initially, *O. humilus* became the dominant species, reaching maximum levels of parasitism in 1915. *D. tryoni* was dominant from 1916 onward, with maximum parasitism recorded in 1918. Total parasitism from 1914 to 1933 ranged between 24.9-56.4% (Willard and Mason 1937). *O. humilus* disappeared from Oahu in the late 1930s, but Clausen et al. (1965) reported it as abundant in the Kona section of the island of Hawaii, equaling or exceeding *D. tryoni* in coffee. Interestingly, *O. humilus* is not reported in more recent literature. The displacement of *O. humilus* by *D. tryoni* may be due to a competitive advantage by the strongly mandibulate larvae of the latter species (Pemberton and Willard 1918).

After its establishment, *T. giffardianus* parasitized up to 25.3% of *C. capitata* larvae, averaging 6.3% between 1914-1933 (Willard and Mason 1937). Subsequent to Clausen et al. (1965), it had not been reported until Ramadan and Wong (1990) found it to be abundant in the Kula area of Maui. Purcell et al. (1994) found that while this

species is absent from guavas collected on the tree, it is common in fruit remaining on the ground for 4-9 days. Purcell (submitted) reports that another eulophid, *Aceraneuromyia indica* Silvestri, is established on all major islands, but appears to be less abundant than *T. giffardianus*.

Until the early 1950s, *D. fullawayi* was readily recovered from coffee and peach (Bess et al. 1961). Haramoto and Bess (1970) found this species only in coffee plantations in Kona, Hawaii. It has not been reported since.

Between 1947-1952, many species of parasitoids were introduced to Hawaii for the control of *B. dorsalis* (Clausen et al. 1965). Of these only four species of opiine braconids became permanently established: *Fopius (Biosteres) arisanus* (Sonan), *Diachasmimorpha longicaudata* (Ashmead), *Fopius (Biosteres) vandenboschi* (Fullaway), and *Psyttalia incisi* (Silvestri).

There was an interesting succession of parasitoids between 1948-1950. Initially, *D. longicaudata* was the dominant species. During the late summer and fall of 1949, *F. vandenboschi* increased in abundance, and by the end of the year had become far more numerous than *D. longicaudata* (Bess et al. 1950). During 1950, *F. arisanus* increased dramatically, and on Oahu constituted 99.4% of the total parasitism in December (van den Bosch et al. 1951). The total parasitism also increased, to approximately 80% (van den Bosch et al. 1951). *F. arisanus* has remained the dominant parasitoid ever since.

Several factors may explain this successive displacement. *F. arisanus* attacks the egg of its host (van den Bosch and Haramoto 1951), *F. vandenboschi* first-instar larvae, and *D. longicaudata* second and third-instar larvae. While all eggs are accessible to *F. arisanus*, some larvae may escape parasitism by burrowing into the fruit pulp, especially

in large fruit (Sivinski 1991). This phenomenon would increase with older larvae, thus putting *D. longicaudata* at a disadvantage. Additionally, *F. arisanus* larvae inhibit the development of *F. vandenboschi* and *D. longicaudata*, and those of *F. vandenboschi* inhibit the development of *D. longicaudata* (van den Bosch and Haramoto 1953). This inhibition is apparently by means of physiological suppression and not physical injury (van den Bosch and Haramoto 1953). The early predominance of *D. longicaudata* was apparently enhanced by the disproportionate release of large numbers of individuals of this species (van den Bosch et al. 1951).

Note that Palacio et al. (1991) found no evidence of physiological suppression in a study on competition among *F. arisanus*, *D. longicaudata* and *Fopius (Biosteres) persulcatus* Silvestri. Instead, they found that *D. longicaudata* was a superior competitor to both *F. arisanus* and *F. persulcatus*, with *F. persulcatus* being superior to *F. arisanus*, indicating physical competition among first-instar larvae. They further reported that *D. longicaudata* did not discriminate between parasitized and unparasitized hosts, while *F. persulcatus* avoided superparasitism. However, Lawrence et al. (1978) demonstrated that *D. longicaudata* does avoid superparasitism when provided with large numbers of hosts.

F. arisanus, *D. longicaudata*, and *F. vandenboschi* develop not only on *B. dorsalis*, but also on *C. capitata*. The reduced abundance of *C. capitata* in the early 1950s was partially attributed to the effects of these parasitoids, particularly *F. arisanus* (Bess 1953). *P. incisi* does not develop on *C. capitata* (Stark et al. 1994).

D. tryoni does not develop on *B. dorsalis*, except in cases of multiparasitism involving *D. longicaudata* (Ramadan et al. 1994a). However, it develops on two species

of gall-forming tephritids, the eupatorium gall fly, *Procecidochares utilis* Stone, and the lantana gall fly, *Eutreta xanthochaeta* Aldrich (Haramoto and Bess 1970).

F. arisanus is the dominant parasitoid of both *B. dorsalis* and *C. capitata* in Hawaii. However, other species may constitute a large part of the total parasitism under certain circumstances. Wong et al. (1984) and Wong and Ramadan (1987) studied the parasitoid fauna on both species of fruit flies in the Kula area of Maui. In these studies, fly pupae were not separated, so the various parasitoid species could not be attributed to a specific fly species. *D. longicaudata* and *D. tryoni* were quite common on loquats and peaches, occasionally surpassing *F. arisanus* in abundance. For example, *D. longicaudata* accounted for 34.9% of the total parasitism in 1979 from peaches, and 33.4% in 1984 from loquats, and *D. tryoni* accounted for 32.7% in 1980 from loquats. *P. incisi* and *F. vandenboschi* accounted for 1.6% and 0.2 of the total parasitism, respectively.

At a site at 1200 m elevation on Hawaii island, *D. tryoni* was the dominant species, and often the only one recovered (M. Purcell pers. comm.). Dominance at high altitudes may be related to an observation by Pemberton and Willard (1918) that mature *D. tryoni* larvae enter a winter diapause within host puparia.

Several additional studies have reported relative abundance of *B. dorsalis* parasitoids. Vargas et al. (1990) reported that in ripe fruit in an agricultural area, *D. longicaudata* and *P. incisi* constituted 3.9-5.5% and 0.4-2.3% of the total parasitism, respectively. Stark et al. (1991) determined the abundance of parasitoids in commercial guava by canopy fogging. *D. longicaudata, P. incisi*, and *F. vandenboschi* accounted for 9-10%, 2-10%, and 0.25-1% of the total parasitism, respectively. Vargas et al. (1993)

report that these three species were more common in orchards than in wild guava. They suggest that two possible factors contributing to this observation may be high tree densities and abundance of rotting fruit in commercial guava orchards. Vargas et al. (1993) point out that fruit type influenced parasitoid abundance. *F. vandenboschi* represented 8.8% of the total parasitoids collected from passion fruit in 1988. Small fruits such as Surinam cherry and false kamani produced many *P. incisi*, while *D. longicaudata* was often common in mango (32.2% in 1988).

Purcell et al. (1994) sampled guava fruit from the tree and the ground. They found that *D. longicaudata* abundance increased as fruit aged on the ground, and *P. incisi* was recovered only from fruit on the ground at least 4 days. This suggests that these parasitoids forage on fruit on the ground, and sampling fruit only from the tree would underestimate their abundance. *F. vandenboschi* abundance (less than 3% of total parasitoids) was unaffected by fruit ripeness.

Vargas et al. (1995) studied abundance of Mediterranean and oriental fruit flies and their parasitoids in newly-planted coffee fields. Although parasitism of *C. capitata* by *F. arisanus* was apparently density-dependent, low parasitism (33.1-37.6%) was observed. Interestingly, *F. arisanus* parasitized a greater percentage of *C. capitata*, the more common host, than *B. dorsalis*. On Oahu, *F. arisanus* appeared to be inefficient in parasitizing hosts at low population densities (Harris and Lee 1987).

The opiine braconid *Psyttalia fletcheri* (Silvestri) was introduced in 1915-1916 for control of *B. cucurbitae* (Clausen et al. 1965). It is the only significant parasitoid of *B. cucurbitae* in Hawaii (Nishida 1955). This species was more common on the wild hosts *Momordica balsamina* L. and *M. charantia* L. than on cultivated hosts, with parasitism

levels of up to 50% during favorable seasons (Nishida 1955). Parasitism was highest in winter and lowest in summer (Nishida 1955). Larvae in vines were more highly parasitized than larvae in fruits, possibly because in the latter they could escape parasitism by penetrating deeply into the pulp (Nishida 1955). This may also explain the low parasitism on large cultivated fruits. Parasitism in cultivated fruits was higher in very weedy fields, suggesting that *P. fletcheri* favors weedy situations (Nishida 1955). Harris and Lee (1989) suggest that the absence of *P. fletcheri* from Molokai may be due to unfavorable high winds on that island.

Liquido et al. (1994) report very low (less than 1%) parasitism of *B. latifrons* by *D. longicaudata* and *Tetrastichus* sp.

Anastrepha **and** ***Ceratitis*** **in Tropical and Subtropical America**

The genus *Anastrepha* includes 184 described species ranging from the southern United States to northern Argentina (Aluja 1994). At least 54 species occur in Panama (Stone 1942) and 23 in Mexico (Aluja et al. 1987). Biological knowledge is basically restricted to seven economically important species: *fraterculus*, *grandis*, *ludens*, *obliqua*, *serpentina*, *striata*, and *suspensa* (Aluja 1994).

Several studies of *Anastrepha* abundance have been conducted in Chiapas, southern Mexico. Celedonio-Hurtado et al. (1995) trapped flies in orchards of various fruit species. Fruit fly species composition varied among orchards, with 1 or 2 predominant species representing 43-86% of all individuals. For example, in sapodilla, *Achras zapota* L., 86% of all flies trapped were *A. serpentina* (Wiedemann), while in chalum, *Inga micheliana* Harms, 66% were *A. distincta* Greene and 25% *A. ludens* (Loew). Rainfall could not explain population fluctuations, and the authors conclude that

host fruit availability is the most important factor affecting adult populations. *A. obliqua* (Macquart) and *A. ludens* are the predominant species in mango, with *A. obliqua* being more common at lower elevations and *A. ludens* at higher elevations (Aluja et al. 1987, 1990, 1996). In another study conducted in a coffee producing area of the same state, *A. ludens* was the most abundant species with 60% of trapped flies, followed by *A. distincta* and *A. fraterculus* (Wiedemann) with 22 and 12%, respectively (Malo et al. 1987). The occurrence of the latter two species was related to the abundance of *Inga* spp., the main host of *A. distincta*, and coffee, a minor host of *A. fraterculus*, in the study area.

Studies in other countries showed similar tendencies. In Costa Rica, *A. obliqua* was associated with mango and other Anacardiaceae, *A. striata* Schiner with guava and other Myrtaceae, and *A. serpentina* with species of Sapotaceae (Jirón and Hedstrom 1988, 1991). Soto-Manitiu and Jirón (1989) found that the maximum abundance of each species coincides with the fruiting season of their respective host plants. Most *A. obliqua* emerge just after first rains, coinciding with the mango fruiting season. In citrus orchards in Belize, the seasonal increase in numbers of *A. ludens* trapped was derived mainly from infestations in grapefruit (Houston 1981).

In Brazil population dynamics of *A. fraterculus* has been related to host fruit availability (Malavasi and Morgante 1981). Nascimento et al. (1982) report that *A. obliqua* was predominant in citrus orchards, and *A. fraterculus* in localities with tropical hosts, especially guava. While the occurrence of flies in citrus was related to host availability, no such relationship was observed with tropical hosts. Trapping was related to mean and minimum temperature and relative humidity. Fehn (1982) studied the population dynamics of *Anastrepha* spp. in peach orchards at three locations in two

seasons. He found relationships with various meteorological factors, including temperature, relative humidity, rainfall and wind velocity, at some locations and seasons but not others. However, he suggests that availability of alternative hosts may be the principal factor affecting population dynamics.

C. capitata invaded Costa Rica in 1955 and has since spread to all of Central America (references in Wharton et al. 1981), and into South America to Brazil (Aguiar and Menezes 1996). It comprised 5 and 19% of fruit flies collected in Costa Rica and Brazil, respectively (Jiron and Hedstrom 1988, Aguiar and Menezes 1996).

Several species of parasitoids were released for the control of *C. capitata* in Central America (Gilstrap and Hart 1987). Of these, three species--*D. longicaudata*, *F. arisanus* and the eulophid *A. indica*--were recovered by Wharton et al. (1981) in Costa Rica. In this study, *D. longicaudata* and *F. arisanus* were the dominant parasitoids of *C. capitata*, while *A. indica* and *D. longicaudata* were the most common on *Anastrepha* spp. Native parasitoids occurred in much smaller numbers. For example, parasitism of *Anastrepha* spp. by the opiines *Doryctobracon areolatus* (Szepligeti) and *Utetes anastrephae* (Vier.) was only 0.2 and 0.05%, respectively. In a later study, Jirón and Mexzon (1989) report that *D. areolatus* was the most abundant and widespread species. In Guatemala, *D. longicaudata* was reported to be the most common parasitoid of *C. capitata*, while that of *Anastrepha* spp. was *Doryctobracon crawfordi* (Viereck), followed by *D. areolatus* and *U. anastrephae* (Eskafi 1990). The combined parasitism in this study was very low (<2%) for all fruits except Surinam cherry with 8% parasitism.

Various exotic fruit fly parasitoids were introduced into Mexico in the 1950s (Jiménez-Jiménez 1956, 1958). Of these, *D. longicaudata* and *A. indica* were established

(Clausen 1978). Several systematic surveys of *Anastrepha* parasitoids were subsequently conducted, producing very different results concerning the relative abundance of parasitoid species. In an area of mixed cultivation in the State of Chiapas in southern Mexico, Aluja et al. (1990) found that the most abundant parasitoid was *D. longicaudata*. However, in a native tropical community in the State of Veracruz, *D. areolatus* and *U. anastrephae* represented 59 and 17%, respectively, of the total parasitism, while *D. longicaudata* was not recovered at all (Hernandez-Ortiz et al. 1994). Lopez et al. (submitted) confirmed that *D. areolatus* is the most common species in Veracruz, representing 43% of all parasitoids recovered from various habitats. It also had the widest host breadth of all parasitoid species. In an earlier study in the State of Nuevo León in northeastern Mexico, Gonzalez-Hernandez and Tejada (1979) reported that the most common parasitoid was *D. crawfordi*, followed by *D. areolatus*. Interestingly, in Veracruz *D. crawfordi* was common only in citrus (Lopez et al., submitted).

Exotic parasitoids also were introduced into other locations in the Americas for the control of *Anastrepha* species. *D. longicaudata* was introduced to Trinidad in 1974 (Bennett et al. 1977). The following year it was the most common parasitoid recovered, surpassing the native *D. areolatus*. In Argentina, *D. longicaudata* and *A. indica* were reported as established (Ovruski and Fidalgo 1994).

Several studies in Brazil report that *D. areolatus* was by far the most abundant parasitoid of *Anastrepha* species. Leonel et al. (1995) found that 70% of parasitoids emerging from samples collected in 10 states were *D. areolatus*. The alysiine *Asobara anastrephae* (Muesebeck) was the second most common species with 19% of the total parasitism, and *U. anastrephae* the third most common with 10%. In the state of São

Paulo alone, *D. areolatus* and *U. anastrephae* constituted 84 and 6% of all parasitoids, respectively (Leonel et al. 1995). In Itaguai, Rio de Janeiro, 89% of all parasitoids collected were *D. areolatus*, with *U. anastrephae* accounting for an additional 8% (Aguiar-Menezes and Menezes 1997). In Amazonas State, *D. areolatus* was found to be the dominant parasitoid in rural locations while *Opius* sp. nr. *bellus* dominated in urban areas (Canal D. et al. 1994, 1995). Finally, *D. areolatus* was the dominant parasitoid of *Anastrepha zenildae* Zucchi in the State of Rio Grande do Norte (Araujo et al. 1996).

D. areolatus also was the most common parasitoid reported from Venezuela, accounting for 33% of the parasitism (Katiyar et al. 1995). *U. anastrephae* was the fourth most common species with 7%. Ovruski (1995) reports low levels of parasitism from Tucumán province, Argentina, with *D. areolatus* emerging from less than 2% of *Anastrepha* spp. puparia. Earlier studies by Nasca (1973) and Fernández de Aráoz and Nasca (1984) also reported *D. areolatus* (as *Opius tucumanus* or *Doryctobracon tucumanus*) from the same province.

Sivinski et al. (1997) analyzed the distribution of parasitoids of *Anastrepha* spp. within tree canopies in Mexico. Several tendencies were reported. Parasitism by *U. anastrephae* was observed only in a narrow range of small host fruits. The efficiency (proportion of larvae attacked in a fruit) of *D. longicaudata* compared to that of other parasitoids increased with fruit size. Parasitism by *D. areolatus* decreased during fruiting periods of individual trees as the season changed from rainy to dry. Negative relationships in parasitism were observed between *D. areolatus* and *U. anastrephae*, while the introduced *D. longicaudata* and native *D. crawfordi* tended to overlap.

Bactrocera oleae in Southern Europe

The olive fly, *Bactrocera oleae* (Gmelin) is native to Africa and currently distributed throughout the Mediterranean basin and the Middle East (Clausen 1978). The braconid *Psyttalia concolor* (Silvestri) was introduced to Italy from North Africa in 1914, and again in 1917-1918, 1923 and 1934 (Clausen 1978). It was also established in France and Greece (Clausen 1978). Inundative releases have been performed at various locations and have proven to be quite successful in reducing fly populations (e.g., Monastero and Delanoue 1966, Kapatos et al. 1977). While it is established in southern Italy, attempts at establishment in more northern regions have failed (e.g., Raspi and Loni 1994).

Bactrocera tryoni in Australia

The Queensland fruit fly, *Bactrocera tryoni* (Froggatt), is native to Australia. Toward the southern fringe of its permanent distribution, there was a significant correlation between summer rainfall and peak fly numbers (Bateman 1972). The effect was thought to be mediated through a reduction in fecundity and immigration, and high mortality among adults emerging through dry soil in dry years.

Several species of exotic parasitoids were introduced to Australia (Snowball et al. 1962). Only *F. arisanus* persisted on the Australian mainland and *D. longicaudata* on Lord Howe Island, even though both species were initially established at both locations (Snowball and Lukins 1964). At most locations, native parasitoids were uncommon relative to *F. arisanus*. Snowball and Lukins (1964) suggest that low winter temperatures may limit the distribution of *F. arisanus* in southern Australia. Snowball (1966)

concludes that factors other that host availability may account for lower and more variable parasitism at higher latitudes, again suggesting some temperature effect.

Conclusion

Factors affecting distribution of fruit flies and their parasitoids could be put into three main categories: abiotic factors, host availability and competition.

The most commonly mentioned abiotic factors are temperature and precipitation. Temperature may be important at limiting distribution at high latitudes, as was suggested for *F. arisanus* in southern Australia. Winter temperatures may also limit parasitoid distribution in Florida, given that these parasitoids originate in tropical regions and may not be adapted to cold temperatures.

The factor most commonly mentioned as affecting distribution and abundance of tropical fruit flies and their parasitoids is host fruit availability. In addition to many studies from Hawaii and tropical America noted above, Tan and Serit (1994) reached similar conclusions regarding *B. dorsalis* in Malaysia. Even in cases in which population dynamics appear to follow temperature changes, several authors have suggested an indirect effect of temperature, through its influence in host availability.

Interspecific interactions among parasitoids may be very complex. Examples of successive replacement of parasitoid species in Hawaii have been regarded as classic examples on competitive displacement. Mechanisms suggested have involved competition among larval stages within fruit, including either physical interaction among larvae or physiological suppression. Additionally, parasitoids attacking early stages replaced parasitoids attacking later stages. It was suggested that earlier stages are more

exposed to parasitoids because they are situated closer to the fruit surface, thus giving the former species an advantage. This mechanism may be irrelevant in Florida, as the three parasitoid species present in the state, namely *D. areolatus*, *D. longicaudata* and *U. anastrephae*, apparently all attack late-instar larvae.

Effects of Temperature and Occurrence of Diapause

The distribution of tropical fruit flies in warm temperate climates can be limited by temperature. Therefore, the determination of low temperature tolerance is important. Messenger and Flitters (1954) used environmental chambers to simulate the climates of locations in the continental United States. They determined that *C. capitata*, *B. cucurbitae*, and *B. dorsalis* could successfully reproduce in most of Florida and along the Gulf coast, and possibly southern California. Flitters and Messenger (1965) stated similar conclusions for *A. ludens*. Meats (1981) and O'Loughlin et al. (1984) determined that the Queensland fruit fly, *Bactrocera tryoni* (Froggatt), could establish permanent, low-density populations in southern Australia.

Levya-Vazquez (1988) used a degree-day model to estimate lower thresholds and thermal constants for *A. ludens*. The lower thresholds for the various immature stages ranged from 9.4-14.1°C. Thomas (1997) found that pupal duration in the field closely fit this laboratory-based model. The puparial stage may be prolonged up to three months in the winter, but there was no evidence of a winter diapause. Larval development time was variable and did not agree well with the model.

Christenson and Foote (1960) reviewed the occurrence of diapause in fruit flies. While diapause is typical of most North American *Rhagoletis* spp., most tropical and subtropical species are not known to undergo diapause.

Prescott and Baranowski (1971) determined the temperature tolerances for *A. suspensa*. Eggs failed to hatch below 12°C or above 33°C. No emergence was observed at 10 and 12°C, although pupae were still viable at 12°C when the experiment was terminated. The calculated development threshold was 10°C and the optimal development temperature approximately 25°C for all immature stages.

Ashley et al. (1976) studied adult emergence of *A. suspensa* and *D. longicaudata* between 22-32°C. Both flies and parasitoids had high levels of mortality above 28°C. In contrast Darby and Kapp (1934) report that *A. ludens* has greater tolerance than its parasitoid *D. crawfordi* at both high and low temperatures. No emergence was observed for *D. crawfordi* at 12 and 30°C and for *A. ludens* at 10 and 31°C.

Loni (1997) studied the effects of temperature on the development of *P. concolor*. Adult emergence was greatest between 18-25°C, markedly reduced at 15 and 28°C, and zero at 13 and 33°C.

Pemberton and Willard (1918) recorded diapause for *D. tryoni* and *D. fullawayi*. Darby and Kapp (1934) observed delayed emergence in several individuals of *D. crawfordi*. Clausen et al. (1965) reported diapause in *D. longicaudata* strains collected from areas having cool winters. Ashley et al. (1976) observed an increase in delayed emergence of *D. longicaudata* larvae at the lowest temperature (22°C) and likewise with low moisture concentration. Finally, Aluja et al. (submitted) recorded diapause in Mexican populations of *D. areolatus*, *D. longicaudata* and *U. anastrephae*, and also in *Aganaspis pellenaroi* (Brethes) and *Odontosema anastrephae* Borgmeier (Hymenoptera: Eulophidae).

In conclusion, temperature tolerances could determine the limits of distribution for fruit flies and their parasitoids. Laboratory studies of temperature effects on Caribbean fruit fly parasitoids could help ascertain the influence of temperature on their distribution in Florida.

CHAPTER 3
LARGE-SCALE DISTRIBUTION PATTERNS OF CARIBBEAN FRUIT FLY PARASITOIDS IN FLORIDA

Studies from many geographical regions have indicated that distribution of fruit flies and their parasitoids may be affected by a variety of factors, including temperature, precipitation, host fruit availability, and interspecific competition (Chapter 2). Parasitoids may themselves be affected by host fly abundance.

In addition to mean or extreme temperature and precipitation, parasitoids may be influenced by the variance of these factors. In particular, the variability of abiotic factors among months could affect the temporal dynamics of hosts. Fruit yield is highly dependent on environmental factors, and can be adversely affected by temperatures or rainfall that are periodically higher or lower than optimal (Petr 1991, Raper and Kramer 1983). High variance in these abiotic factors would lead to greater variability in the temporal availability of hosts. Parasitoid species may differ in their ability to survive through periods of low host abundance.

Three species of parasitoids are commonly recovered from the Caribbean fruit fly, *Anastrepha suspensa* (Loew), in Florida: *Diachasmimorpha longicaudata* (Ashmead), *Doryctobracon areolatus* (Szepligeti) and *Utetes anastrephae* (Viereck) (Hymenoptera: Braconidae: Opiine). Studies conducted at several locations in Florida suggest that distribution of parasitoid species may differ at various sites (see Chapter 1).

The objective of this chapter was to determine the parasitoid distribution throughout central and southern Florida, and identify abiotic and biotic factors possibly influencing this distribution.

Materials and Methods

Fruit Sampling

Host fruits of *A. suspensa* were collected in 23 towns in central and southern Florida (Figure 3-1). Sample sites were chosen to represent various regions of the peninsula. Thus samples were collected from 5 sites along the Atlantic coast from Melbourne (28.1° N) to Miami (25.8° N), 7 sites along the Gulf of Mexico coast from Tampa (28.0° N) to Naples (26.1° N), and 11 sites in the interior from Dade City (28.4° N) to Belle Glade (26.7° N) and LaBelle (26.8° N). Interior sites were situated along various north-south routes, e.g., US 17 (Lakeland, Wauchula and Arcadia) and US 27 (Haines City, Lake Wales, Lake Placid and Belle Glade). Clewiston, on the south-west coast of Lake Okeechobee, and Immokalee, 37 km south of LaBelle, were not sampled because of previous mass releases of *D. longicaudata* at these locations (Sivinski et al. 1996). Note that there are no interior towns south of those indicated due to the presence of the Everglades.

Sampling was not always limited to the town indicated, and often included collections in adjacent towns. Many Melbourne samples were actually collected in southern Brevard County, and St. Petersburg samples were collected throughout Pinellas County. Lake Placid samples include some from Sebring, and Punta Gorda includes

Figure 3-1. Fruit sample collection sites.

samples from Port Charlotte. On the other hand, two large counties had more than one collection site. Haines City, Lakeland and Lake Wales are all in Polk County, while both West Palm Beach and Belle Glade are in Palm Beach County.

Samples were collected in August 1994, and monthly from January-September 1995. Additional monthly samples were collected at Melbourne, Bradenton, Venice and Okeechobee from March-May 1996 and at St. Petersburg in May 1996. Sampling was not performed from October through December, because at the majority of sites primary host fruits are uncommon during this period in most years (Tim Holler, pers. comm.). All samples were collected within a single week each month. Sampling at Ft. Pierce was conducted by Tim Holler, USDA-APHIS-PPQ, in March and May 1993, prior to augmentative releases of *D. longicaudata*. Sampling at most sites during 1994 and 1995 was performed by the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Bureau of Plant Inspection. Sampling at other sites during 1994 was by USDA-APHIS.

Fruits sampled included loquat (*Eriobotrya japonica* (Thunb.)), Surinam cherry (*Eugenia uniflora* L.), Cattley guava (*Psidium cattleianum* Sabine) and common guava (*Psidium guajava* L.). Loquat samples were collected from January-April, most Surinam cherry samples from April-June, most Cattley guava from July-August, and most common guava from August-September. Note that additional fruiting periods may occur, especially at southern sites. Up to 12 samples were collected for each site during a single month. Each sample included fruits collected from a single tree. Fruits collected were ripe and usually without holes caused by beetles or exiting larvae. They were preferably collected from the tree, but occasionally supplemented with fruits from the ground.

Numbers of samples and total fruits collected at various sites are detailed in Table 3-1. Total sample numbers varied widely among sites, ranging from 17 samples collected at Ft. Pierce to 102 at LaBelle. The number of samples collected was dependent primarily on availability of host fruit. Note that the efficiency of fruit sampling may have varied among sites, as it was often conducted by different personnel at various sites. Cattley guava was the least commonly collected host, with 83 samples, compared with 549, 377 and 290 samples of loquat, Surinam cherry and common guava, respectively.

Fruits were placed within a bucket upon a metal screen. The bucket had holes for ventilation. It was covered with a plastic lid and its inside was lined with cloth to prevent entry of insects after fruit collection and escape of insects emerging from the fruit sample. Moist fine vermiculite (ca. 15 ml water per 100 cm^3 vermiculite) was placed at the bottom of the bucket. Mature fruit fly larvae exited the fruit and pupated in the vermiculite.

At the end of each sampling week, buckets were collected from various locations and transported to Gainesville. Buckets were maintained at 25.5° C, except in 1995 when they were kept in a warehouse at ambient temperatures. Puparia were sifted from the vermiculite 13-15 days after fruit collection, and transferred to 250 ml plastic containers. These containers were initially covered with a solid lid, which was replaced after ca. one week with a screened lid. This was done to assure that the vermiculite did not dry out, but was also not so moist as to allow development of fungi. Containers were maintained at 25.5° C and ambient humidity.

Table 3-1. Total number of host fruit samples and total fruits collected at various sites.

Site	Loquat		Surinam cherry		Cattley guava		Common guava	
	Samples	Fruits	Samples	Fruits	Samples	Fruits	Samples	Fruits
Arcadia	35	1162	11	1076	3	94	10	51
Belle Glade	8	139	31	1202	1	22	31	100
Bradenton	32	873	24	1433	1	1	7	59
Dade City	29	1017	0	0	0	0	6	13
Ft. Lauderdale	9	321	30	1469	2	50	13	47
Ft. Myers	27	854	14	1090	19	510	5	50
Ft. Pierce	6	610	10	1550	0	0	1	22
Haines City	22	567	9	349	0	0	0	0
LaBelle	39	1272	28	2021	5	210	30	226
Lakeland	35	663	16	614	4	100	26	122
Lake Placid	37	1261	19	1534	3	98	11	75
Lake Wales	21	713	18	916	0	0	29	192
Melbourne	42	1241	21	1181	4	140	17	166
Miami	3	72	12	553	2	27	31	171
Naples	26	630	23	1129	24	806	3	---
Okeechobee	21	713	20	1385	0	0	5	22
Punta Gorda	25	645	19	1160	10	353	0	0
St. Cloud	12	351	16	621	0	0	21	191
St. Petersburg	29	685	11	736	0	0	10	28
Tampa	29	561	0	0	0	0	8	---
Venice	15	441	20	1615	0	0	0	0
Wauchula	40	1494	15	1185	2	61	22	133
W. Palm Beach	7	148	10	345	3	41	5	22

Flies and parasitoids emerged within the containers, and were counted when no more live insects were observed. Parasitism levels for each species were calculated for each sample as the ratio between the number of parasitoids of the relevant species emerging and the sum of all flies and parasitoids emerging. This assumes that neither the flies nor the parasitoids diapause, and that mortality levels of the fly pupae and immature parasitoids are similar. In Florida, emergence rates of pupae held indoors under controlled temperature and humidity are typically ca. 90% (Sivinski, pers. comm.), so that it is unlikely that a significant proportion of parasitoids undergo diapause. In contrast, diapause appears to be quite prevalent among parasitoids held under semi-natural conditions in Mexico (Aluja et al., submitted). Note that true levels of parasitism are underestimated, because fruit removed from the field include host eggs and larvae that may have been parasitized if left in place. However, comparisons of parasitism levels as measured should reflect relative abundance.

Abiotic Environmental Data

Temperature and precipitation data were obtained from the Southeast Regional Climate Center, Columbia, South Carolina. Weather stations exist in most of the towns included in the study. However, there are no data for the vicinity of Dade City and Haines City. Data from Winter Haven and Avon Park were used to represent Lake Wales and Lake Placid–Sebring, respectively. The following variables were obtained: mean annual temperature, mean minimum temperature for the coldest month of the year, mean maximum temperature for the warmest month of the year, extreme annual minimum and maximum temperatures, and annual precipitation (Table 3-2).

Table 3-2. Mean precipitation and temperature values for towns in central and southern Florida, for the years 1980-1996. Data were obtained from the Southeast Regional Climate Center, Columbia, South Carolina.

Town	Annual precipitation (mm)	Mean annual temp (°C)	Mean minimum temp (°C)[a]	Extreme minimum temp (°C)	Mean maximum temp (°C)[b]	Extreme maximum temp (°C)
Arcadia	1341	22.2	8.0	-3.0	33.4	36.5
Avon Park	1263	22.3	7.6	-3.0	33.4	36.1
Belle Glade	1290	22.8	9.6	-0.8	33.3	35.5
Bradenton	1412	22.8	9.0	-1.8	33.6	36.0
Ft. Lauderdale	1672	24.4	13.9	2.9	32.3	35.3
Ft. Myers	1390	23.9	11.3	0.7	33.9	36.6
Ft. Pierce	1403	23.0	9.3	-1.8	33.4	36.5
LaBelle	1310	23.3	9.0	-1.6	34.1	36.8
Lakeland	1320	23.1	9.1	-3.2	34.6	37.2
Melbourne	1243	22.5	9.2	-1.5	32.5	36.0
Miami	1509	24.8	14.3	3.7	32.8	35.8
Naples	1325	23.8	11.3	0.6	33.5	35.9
Okeechobee	1224	23.1	8.3	-0.9	30.5	36.7
Punta Gorda	1309	23.5	10.2	-0.9	33.8	36.1
St. Cloud	1268	22.6	8.6	-2.6	33.4	36.0
St. Petersburg	1270	23.3	11.3	1.1	32.8	35.8
Tampa	1133	22.7	9.2	-1.8	33.0	35.5
Venice	1140	22.9	8.8	-0.9	33.4	35.4
Wauchula	1300	22.8	9.7	-2.6	34.0	36.4
W. Palm Beach	1609	24.1	12.8	1.8	32.7	35.5
Winter Haven	1286	23.0	9.2	-2.2	34.0	36.7

[a]For the coldest month of the year.
[b]For the warmest month of the year.
Temp = temperature.

The annual variance of the following monthly values were calculated: mean temperature, mean minimum temperature, mean maximum temperature, extreme minimum temperature, extreme maximum temperature and precipitation. The mean values of these variables for the years 1980-1996 were used for analysis.

Host Fly and Host Plant Data

A. suspensa catch data from McPhail traps were obtained from the North Florida Research and Education Center, Quincy, Florida. Trapping was performed by the U.S. Department of Agriculture and by the Florida Department of Agriculture and Consumer Services, Division of Plant Industry. Only trapping data from urban locations were used, in order to conform with parasitoid data, which were also from urban sites. Data were available in the form of monthly numbers of flies per trap for various counties, and exact identity of the town(s) where traps were situated was unknown. Following are the counties for which data were available, and in parentheses the fruit collection site to which they were related in subsequent analyses: Brevard (Melbourne), Broward (Ft. Lauderdale), Charlotte (Punta Gorda), Collier (Naples), Dade (Miami), De Soto (Arcadia), Hardee (Wauchula), Highlands (Lake Placid), Hillsborough (Tampa), Lee (Ft. Myers), Manatee (Bradenton), Okeechobee (Okeechobee), Palm Beach (Belle Glade), Pinellas (St. Petersburg), Polk (Lakeland), Sarasota (Venice), St. Lucie (Ft. Pierce). Trapping data were for the years 1992-1996, except for Brevard, Broward, Dade, Palm Beach and Pinellas Counties, for which data were for 1990-1996. Variables used for analysis included mean monthly catch, minimal monthly catch, and maximal monthly catch. These were calculated for each year, and the mean annual value for each variable (Table 3-3) used for analysis.

Table 3-3. Numbers of Caribbean fruit flies captured in McPhail traps for various counties in central and southern Florida. Traps were maintained by the Florida Division of Plant Industry and the U. S. Department of Agriculture. Data were obtained from the North Florida Research and Education Center, Quincy, Florida.

County (corresponding site)	Mean[a]	Minimum[b]	Maximum[c]
Brevard (Melbourne)	1.4	0	7.8
Broward (Ft. Lauderdale)	24	0.81	115.5
Charlotte (Punta Gorda)	46	0.51	276.7
Collier (Naples)	35.2	0.9	104.8
Dade (Miami)	26.5	1.07	129.4
De Soto (Arcadia)	5.1	0.55	19.0
Hardee (Wauchula)	6.9	0.16	31.0
Highlands (Lake Placid)	14.8	0.66	55.6
Hillsborough (Tampa)	5.5	0.36	28.0
Lee (Ft. Myers)	34.4	2.21	147.7
Manatee (Bradenton)	3.0	0.15	15.5
Okeechobee (Okeechobee)	1.1	0.02	6.1
Palm Beach (Belle Glade)	8.8	0.14	46.2
Pinellas (St. Petersburg)	4.0	0.03	22.6
Polk (Lakeland)	11.8	0.72	52.3
Sarasota (Venice)	19.7	1.22	97.2
St. Lucie (Ft. Pierce)	13.4	1.09	42.9

Mean values for the years 1990-1996 for Brevard, Broward, Dade, Palm Beach and Pinellas counties, and 1992-1996 for other counties.
[a]Mean monthly catch.
[b]Minimum monthly catch.
[c]Maximum monthly catch.

A survey was performed to determine the density of host fruit trees in various towns. Quadrants were chosen from various regions of each town. Previous experience suggested that older middle-class neighborhoods were the best areas for *A. suspensa* hosts. Specific quadrants were picked that appeared on a map to match this designation. Upon arrival, obviously unsuitable quadrants were dismissed, and others chosen from the map to replace them. Four quadrants were sampled in each town, except LaBelle where 5 quadrants were sampled. Host trees were counted during a slow drive through the neighborhood. Thus trees in back yards were counted only if observed from the street. As towns differ in the size and visibility of backyard properties, the number of trees present but not observed per unit area would presumably also differ. Therefore, comparisons of towns based on number of trees counted per unit area may not be reliable. Rather, relative density was estimated as the number of trees observed per km of road. Distances traveled per quadrant ranged from 4.3-14.8 km, but were usually between 5-10 km.

Statistical Analysis

Parasitism data were subjected to an arcsine square root transformation before analysis. All analyses were performed using SAS statistical software.

Environmental factors could be associated with either (1) absolute parasitoid distribution, i.e., presence or absence at various sites, or (2) relative abundance of parasitoids among sites in which they are present, as measured by parasitism level. The factors associated with each response may differ.

Associations of environmental factors with presence or absence of each parasitoid species were analyzed using logistic regression models (SAS Institute 1989). All

temperature, precipitation and fruit tree density factors were tested separately in these analyses.

Associations of temperature, precipitation and host fruit tree density with parasitism levels were analyzed using linear regression models. Models examining parasitism of all species combined included all sites sampled. Models examining parasitism levels of each species separately included only sites in which the relevant parasitoid species was collected. The various fruit types were analyzed separately. Initially, all temperature, precipitation and fruit tree density factors were included, and their relative fit with the model determined by the forward selection procedure (SAS Institute 1989). Ultimately, only the factor best explaining parasitoid abundance remained in the final single linear regression model. In addition to single regression, multiple regression models were examined including all factors significantly related with parasitism levels.

Host fly population levels are not independent of the previously described factors, i.e., temperature, precipitation and host fruit tree density. Therefore, host fly data could not be included as factors in the previous analyses. Separate linear regression models were examined relating parasitism levels with fly trapping variables. All sites were included in this analysis. Thus in this case I did not differentiate between presence or absence of parasitoid species and their relative abundance.

Results

Distribution and Abundance of Parasitoids

Numbers of samples containing parasitoids and numbers of parasitoids emerging for various towns and host fruits are detailed in the Appendix and summarized in Tables 3-4 and 3-5.

With data from all towns combined, parasitism levels were higher in Surinam cherry and Cattley guava than in loquat or common guava for both *D. areolatus* and *D. longicaudata*. For *U. anastrephae*, parasitism levels were higher in Surinam cherry than in any other fruit (Table 3-6). Parasitism by *U. anastrephae* was extremely low in common guava, with only 8 individuals recovered from 4 samples (Table 3-5). These results are consistent with the findings of Sivinski (1991; Sivinski et al. 1997) that smaller fruits have higher levels of parasitism. As expected, the differences in parasitism levels among fruit types is largest for *U. anastrephae*, which has a relatively short ovipositor, and thus less access to larvae deep within large fruits.

Overall, *D. areolatus* was more abundant than *D. longicaudata* in Surinam cherry and common guava, but not in loquat or Cattley guava (Table 3-6). Both species were more common than *U. anastrephae* in loquat and common guava, but mean parasitism levels of *D. longicaudata* and *U. anastrephae* were not significantly different in Surinam cherry or Cattley guava.

With all data combined, it appears that parasitism levels are quite low (Table 3-6). Note, however, that this includes data from sites where certain parasitoid species were totally absent from samples. Even where parasitoids were recovered, many samples did

Table 3-4. Numbers of samples collected and insects emerging for various sites. Each sample includes fruits from a single host tree.

Site	Number of samples					Number of insects emerging			
	Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Arcadia	59	57	27	0	1	3095	589	0	3
Belle Glade	71	63	0	20	9	3462	0	106	27
Bradenton	64	48	0	1	4	1816	0	6	33
Dade City	35	32	0	0	0	672	0	0	0
Ft. Lauderdale	54	48	0	12	9	2746	0	214	59
Ft. Myers	65	59	9	22	19	3092	27	156	79
Ft. Pierce	17	17	0	7	8	1352	0	10	110
Haines City	31	18	1	0	0	281	1	0	0
LaBelle	102	95	42	43	2	3267	768	482	7
Lakeland	81	63	13	0	1	3629	172	0	2
Lake Placid	70	64	23	0	1	2837	356	0	1
Lake Wales	67	59	19	0	0	2500	230	0	0
Melbourne	84	53	0	0	0	961	0	0	0
Miami	48	40	0	11	4	2539	0	81	10
Naples	76	49	2	9	6	1210	5	58	36
Okeechobee	46	40	6	4	1	1748	181	9	7
Punta Gorda	54	36	5	1	3	1479	19	1	11
St. Cloud	49	37	0	0	2	1288	0	0	16
St. Petersburg	50	34	0	0	0	1354	0	0	0
Tampa	37	28	2	0	0	1198	2	0	0
Venice	35	31	1	0	13	2097	1	0	60
Wauchula	79	75	36	0	3	4368	599	0	16
W. Palm Beach	25	19	0	3	1	439	0	51	5

[a]CFF = Caribbean fruit fly.
[b]Da = *Doryctobracon areolatus*.
[c]Dl = *Diachasmimorpha longicaudata*.
[d]Ua = *Utetes anastrephae*.

Table 3-5. Numbers of samples collected and parasitoids emerging for various host fruits. Each sample includes fruits from a single host tree.

Host	Number of samples					Number of insects emerging			
	Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Loquat	549	418	56	30	13	13618	657	418	63
Surinam cherry	377	326	64	55	63	12329	1197	410	377
Cattley guava	83	60	14	15	7	2147	280	97	34
Common guava	290	261	52	33	4	20395	816	249	8

[a]CFF = Caribbean fruit fly.
[b]Da = *Doryctobracon areolatus*.
[c]Dl = *Diachasmimorpha longicaudata*.
[d]Ua = *Utetes anastrephae*.

Table 3-6. Mean percent parasitism (SE) for various host fruits.

Fruit	*D. areolatus*	*D. longicaudata*	*U. anastrephae*
Loquat	2.0 (0.3) B a	1.5 (0.4) B a	0.2 (0.1) B b
Surinam cherry	7.8 (1.1) A a	3.6 (0.6) A b	3.0 (0.6) A b
Cattley guava	7.1 (2.8) A a	5.3 (1.6) A ab	1.1 (0.5) B b
Common guava	2.5 (0.4) B a	1.0 (0.3) B b	0.03 (0.02) B c

Means within a column followed by the same upper-case letter, and means within a row followed by the same lower-case letter, are not significantly different, p=0.05 according to the Waller-Duncan k-ratio t test, and k-ratio=100.

not contain parasitoids (Tables 3-4 and 3-5). When maximum parasitism is considered, it becomes apparent that all three parasitoid species are capable of achieving high levels of parasitism. Over 50% parasitism was observed in certain samples at 6 sites for *D. areolatus*, at 5 sites for *D. longicaudata*, and at 2 sites for *U. anastrephae* (Table 3-7). Additionally, as mentioned above, these observations are almost certainly underestimates of the true parasitism levels.

Mean levels of parasitism for the braconid parasitoids at various sites are summarized in Tables 3-8 through 3-11. At three northern locations, Dade City, Melbourne and St. Petersburg, no parasitoids were found (Table 3-4).

D. areolatus was absent from the Atlantic coast, and also was not collected at Belle Glade, St. Cloud or Bradenton (Figure 3-2). It was most common at interior locations, and relatively rare along the Gulf coast (Figure 3-3). However, distance from the coast was not a significant predictor of *D. areolatus* abundance, perhaps because of its absence at two interior locations. Highest mean parasitism levels observed for various fruits were 6.6% in loquat at Arcadia, 35.8% in Surinam cherry at LaBelle, 79.7% in Cattley guava at Arcadia, and 10.2% in common guava at Arcadia.

D. longicaudata was not collected at interior locations north and west of Lake Okeechobee, or at the most northern locations along both coasts (Figure 3-2). It was uncommon at all locations at the northern end of its distribution, with the exception of LaBelle (Figure 3-4). *D. longicaudata* abundance was significantly greater at lower latitudes in both Surinam cherry and common guava ($F=12.9$, $p=0.002$ and $F=6.5$, $p=0.02$, respectively). Highest mean parasitism levels observed for various fruits were

Table 3-7. Maximum parasitism levels (percent parasitism per sample) in various host fruits at various sites. Includes samples from which at least 10 adult insects were recovered.

Site	Loquat			Surinam cherry			Cattley guava			Common guava		
	Da[a]	Dl[b]	Ua[c]	Da[a]	Dl[b]	Ua[c]	Da[a]	Dl[b]	Ua[c]	Da[a]	Dl[b]	Ua[c]
Arcadia	29.1	0	0	73.5	0	5.6	71.9	0	0	32.4	0	0
Belle Glade	0	0	0	0	35.3	64.3	---	---	---	0	41.2	0
Bradenton	0	0	2.2	0	14.6	35.2	---	---	---	0	0	0
Dade City	0	0	0	---	---	---	---	---	---	0	0	0
Ft. Lauderdale	0	14.1	4.7	0	58.5	61.9	0	0	0	0	17.6	2.9
Ft. Myers	3.8	75.0	9.3	7.1	25.0	21.7	3.8	42.3	6.9	10.8	25.7	3.7
Ft. Pierce	0	3.6	19.6	0	4.4	30.9	---	---	---	0	0.4	0
Haines City	0	0	0	0	0	0	---	---	---	---	---	---
LaBelle	37.7	54.3	0	83.3	72.0	21.1	51.9	15.2	0	55.7	24.3	0
Lakeland	0	0	0	24.1	0	0	10.9	0	0	32.0	0	0.8
Lake Placid	63.2	0	0	90.9	0	1.2	65.8	0	0	20.9	0	0
Lake Wales	22.6	0	0	81.1	0	0	---	---	---	29.5	0	0
Melbourne	0	0	0	0	0	0	0	0	0	0	0	0
Miami	0	3.6	3.6	0	51.5	15.2	0	0	0	0	12.5	0
Naples	0	1.0	7.1	6.0	31.3	7.5	6.7	53.3	15.3	0	14.8	0
Okeechobee	0	0	0	67.6	12.2	10.0	---	---	---	0	3.1	0
Punta Gorda	4.2	0	0	40.0	0	22.6	2.3	2.3	0	---	---	---
St. Cloud	---	---	---	0	0	34.3	---	---	---	0	0	0
St. Petersburg	0	0	0	0	0	0	---	---	---	0	0	0
Tampa	1.0	0	0	---	---	---	---	---	---	0.4	0	0
Venice	0	0	0.7	1.1	0	40.0	---	---	---	---	---	---
Wauchula	32.4	0	0	87.5	0	18.6	---	---	---	55.9	0	0
W. Palm Beach	0	35.9	0	0	20.0	11.6	0	0	0	0	0	0

[a]Da = *Doryctobracon areolatus*. [b]Dl = *Diachasmimorpha longicaudata*. [c]Ua = *Utetes anastrephae*.

Table 3-8. Mean percent parasitism (SE) in loquat for various sites.

Site	*D. areolatus*			*D. longicaudata*			*U. anastrephae*		
Arcadia	6.6 (1.8)	A	a	0	C	b	0	C	b
Belle Glade	0	B		0	C		0	C	
Bradenton	0	B		0	C		0.1 (0.1)	C	
Dade City	0	B		0	C		0	C	
Ft. Lauderdale	0	B		2.0 (2.0)	BC		0.7 (0.7)	C	
Ft. Myers	0.2 (0.1)	AB	b	6.9 (1.1)	AB	a	1.1 (0.5)	BC	ab
Ft. Pierce	0	B		0.7 (0.6)	BC		4.6 (3.3)	A	
Haines City	0	B		0	C		0	C	
LaBelle	4.9 (1.5)	AB	b	10.4 (0.3)	A	a	0	C	c
Lakeland	0	B		0	C		0	C	
Lake Placid	3.1 (1.9)	AB	a	0	C	b	0	C	b
Lake Wales	2.7 (1.4)	AB	a	0	C	b	0	C	b
Melbourne	0	B		0	C		0	C	
Miami	0	B		1.8 (1.8)	BC		1.8 (1.8)	B	
Naples	0	B		0.05 (0.05)	C		0.4 (0.4)	C	
Okeechobee	0	B		0	C		0	C	
Punta Gorda	0.3 (0.3)	AB		0	C		0	C	
St. Cloud	0	B		0	C		0	C	
St. Petersburg	0	B		0	C		0	C	
Tampa	0.05 (0.05)	B		0	C		0	C	
Venice	0	B		0	C		0.06 (0.06)	C	
Wauchula	6.5 (1.5)	AB	a	0	C	b	0	C	b
W. Palm Beach	0	B		7.2 (7.2)	AB		0	C	

Means within a column followed by the same upper-case letter, and means within a row followed by the same lower-case letter, are not significantly different, p=0.05 according to the Waller-Duncan k-ratio t test, and k-ratio=100.

Table 3-9. Mean percent parasitism (SE) in Surinam cherry for various sites.

Site	*D. areolatus*			*D. longicaudata*			*U. anastrephae*		
Arcadia	25.1 (11.1)	ABC	a	0	B	b	0.4 (0.3)	A	b
Belle Glade	0	E	b	12.1 (3.5)	A	a	7.9 (3.3)	A	a
Bradenton	0	E		0.6 (0.6)	B		2.4 (1.6)	A	
Ft. Lauderdale	0	E	a	7.3 (3.2)	AB	a	5.1 (2.7)	A	a
Ft. Myers	0.6 (0.6)	E	b	3.6 (2.4)	B	ab	8.4 (2.8)	A	a
Ft. Pierce	0	E	b	0.7 (0.4)	B	ab	6.8 (3.4)	A	a
Haines City	12.5 (12.5)	CDE		0	B		0	A	
LaBelle	35.8 (6.3)	A	a	13.2 (3.5)	A	b	1.4 (1.1)	A	c
Lakeland	4.6 (2.2)	E	a	0	B	b	0	A	b
Lake Placid	20.2 (6.9)	BCD	a	0	B	b	0.07 (0.07)	A	b
Lake Wales	10.1 (5.5)	DE	a	0	B	b	0	A	b
Melbourne	0	E		0	B		0	A	
Miami	0	E	b	15.4 (7.2)	A	a	1.8 (1.5)	A	b
Naples	0.4 (0.4)	E		2.7 (2.1)	B		7.3 (6.6)	A	
Okeechobee	10.9 (5.1)	DE	a	0.8 (0.7)	B	b	0.6 (0.6)	A	b
Punta Gorda	3.5 (2.8)	E		0	B		2.4 (1.7)	A	
St. Cloud	0	E		0	B		3.8 (2.7)	A	
St. Petersburg	0	E		0	B		0	A	
Venice	0.06 (0.06)	E	b	0	B	b	4.6 (2.0)	A	a
Wauchula	32.4 (8.9)	AB	a	0	B	b	2.0 (1.3)	A	b
W. Palm Beach	0	E		3.5 (2.8)	B		1.7 (1.7)	A	

Means within a column followed by the same upper-case letter, and means within a row followed by the same lower-case letter, are not significantly different, p=0.05 according to the Waller-Duncan k-ratio t test, and k-ratio=100.

Table 3-10. Mean percent parasitism (SE) in Cattley guava for various sites.

Site	*D. areolatus*		*D. longicaudata*		*U. anastrephae*	
Arcadia	79.7 (10.2)	A	0		0	A
Ft. Lauderdale	0	D	0		0	A
Ft. Myers	0.5 (0.3)	D b	8.8 (3.4)	a	1.2 (0.8)	A b
LaBelle	17.9 (11.9)	C	5.7 (3.6)		0	A
Lakeland	3.6 (3.6)	D	0		0	A
Lake Placid	65.8	B	0		0	A
Melbourne	0	D	0		0	A
Miami	0	D	0		10.0 (10.0)	A
Naples	0.6 (0.6)	D	9.8 (5.3)		1.8 (1.4)	A
Punta Gorda	0.3 (0.3)	D	0.3 (0.3)		0	A
W. Palm Beach	0	D	0		0	A

Means within a column followed by the same upper-case letter, and means within a row followed by the same lower-case letter, are not significantly different, $p=0.05$ according to the Waller-Duncan k-ratio t test, and k-ratio=100.

10.4% in loquat at LaBelle, 15.4% in Surinam cherry at Miami, 9.8% in Cattley guava at Naples, and 9.6% in common guava at Ft. Myers.

U. anastrephae was widespread, having been collected at most locations (Table 3-4). Parasitism levels for this species were relatively low, especially at most interior locations (Figure 3-5). Highest mean parasitism levels observed for various fruits were 4.6% in loquat at Ft. Pierce, 8.4% in Surinam cherry at Ft. Myers, 10.0% in Cattley guava at Miami, and 1.0% in common guava at Ft. Myers.

Table 3-11. Mean percent parasitism (SE) in common guava for various sites.

Site	*D. areolatus*			*D. longicaudata*			*U. anastrephae*		
Arcadia	10.2 (4.1)	A	a	0	B	b	0	B	b
Belle Glade	0	B		2.0 (1.4)	B		0	B	
Bradenton	0	B		0	B		0	B	
Dade City	0	B		0	B		0	B	
Ft. Lauderdale	0	B	b	3.5 (1.7)	B	a	0.2 (0.2)	B	b
Ft. Myers	2.4 (2.1)	AB		9.6 (4.4)	A		1.0 (0.7)	A	
Ft. Pierce	0	B		0.4	B		0	B	
LaBelle	7.1 (2.8)	AB	a	3.0 (1.2)	B	ab	0	B	b
Lakeland	2.5 (1.4)	AB	a	0	B	b	0.03 (0.03)	B	ab
Lake Placid	4.9 (2.0)	AB	a	0	B	b	0	B	b
Lake Wales	4.5 (1.8)	AB	a	0	B	b	0	B	b
Melbourne	0	B		0	B		0	B	
Miami	0	B	b	1.3 (0.7)	B	a	0	B	b
Naples	0	B		4.9 (4.9)	AB		0	B	
Okeechobee	0	B		0.8 (0.8)	B		0	B	
St. Cloud	0	B		0	B		0	B	
St. Petersburg	0	B		0	B		0	B	
Tampa	0.05 (0.05)	B		0	B		0	B	
Wauchula	6.2 (2.9)	AB	a	0	B	b	0	B	b
W. Palm Beach	0	B		0	B		0	B	

Means within a column followed by the same upper-case letter, and means within a row followed by the same lower-case letter, are not significantly different, p=0.05 according to the Waller-Duncan k-ratio t test, and k-ratio=100.

The distribution ranges of *D. areolatus* and *D. longicaudata* overlap only within a limited area from Lake Okeechobee to the Gulf of Mexico coast (Figure 3-2). In fact, only at LaBelle are both common (Figure 3-6). Interestingly, LaBelle was among the sites with the highest parasitism levels for both *D. areolatus* and *D. longicaudata*. With all sites included, there was no significant relationship between parasitism levels of *D. areolatus* and *D. longicaudata* in Surinam cherry (Spearman correlation coefficient = -0.27, p= 0.23). However, with LaBelle excluded, parasitism by the two species was negatively related (Spearman correlation coefficient = -0.48, p=0.034). Temporal and spatial dynamics at LaBelle are explored in Chapter 4.

Although *U. anastrephae* is widespread, it is most common at coastal locations and at Belle Glade, i.e., at locations where *D. areolatus* is absent or rare and where *D. longicaudata* is common. With all sites included, parasitism levels of *U. anastrephae* and *D. longicaudata* in Surinam cherry were positively related (Spearman correlation coefficient = 0.53, p=0.014), indicating a similar distribution pattern for both species. Interestingly, when considering only sites where both species were recovered, no significant relationship was observed (Spearman correlation coefficient = -0.02, p=0.96). This suggests that these species do not impact each other on a local level.

With all sites included, no significant relationship was observed between parasitism levels of *U. anastrephae* and *D. areolatus* in Surinam cherry (Spearman correlation coefficient = -0.35, p=0.12). However, when only sites with both species present were considered, parasitism was negatively related (Spearman correlation coefficient = -0.70, p=0.044). This suggests that *U. anastrephae* and *D. areolatus* may have a negative impact on each other. Only at Punta Gorda are these species found

together in similar numbers (Figure 3-6). Note that at this location parasitism by both species was low, with only 19 *D. areolatus* and 11 *U. anastrephae* recovered (Table 3-4). Mean parasitism at Punta Gorda in Surinam cherry was only 3.5% and 2.4% for *D. areolatus* and *U. anastrephae*, respectively (Table 3-9). Thus significant competition at this site was unlikely.

A fourth parasitoid, the eulophid *Aceratoneuromyia indica* Silvestri, emerged from two puparia collected from guava at Belle Glade in February 1995. To my knowledge, this is the only report of this species outside the area of its introduction in Dade County, ca. 140 km to the south.

Host Plant Density

Sample sites varied considerably in the relative density of host fruit trees (Table 3-12). Loquats are most abundant at Dade City, Lake Wales, Melbourne and Tampa, all of which are situated at high latitudes (Figure 3-1). At Dade City, the highest latitude site in this study, other hosts are rare, with only one small Surinam cherry hedge and one common guava located. Lowest numbers of loquats were found at Ft. Myers, Miami, Ft. Lauderdale and Belle Glade. Surinam cherries are most abundant at Miami, St. Petersburg and Belle Glade, Cattley guavas at Naples, Ft. Pierce and LaBelle, and common guavas at LaBelle. Note that at southern coastal towns like Miami, additional tropical host trees occur, which are not included in this survey. The most important of these hosts is tropical almond, *Terminalia catappa* L.

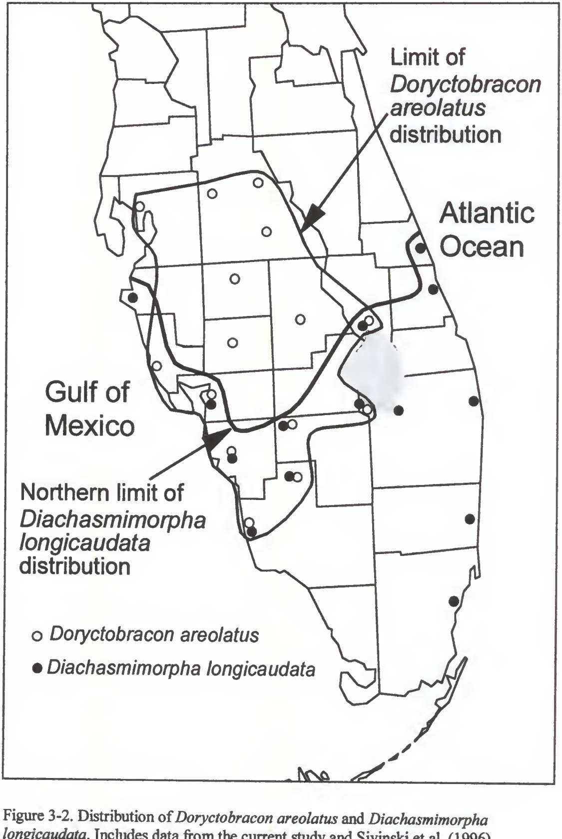

Figure 3-2. Distribution of *Doryctobracon areolatus* and *Diachasmimorpha longicaudata*. Includes data from the current study and Sivinski et al. (1996).

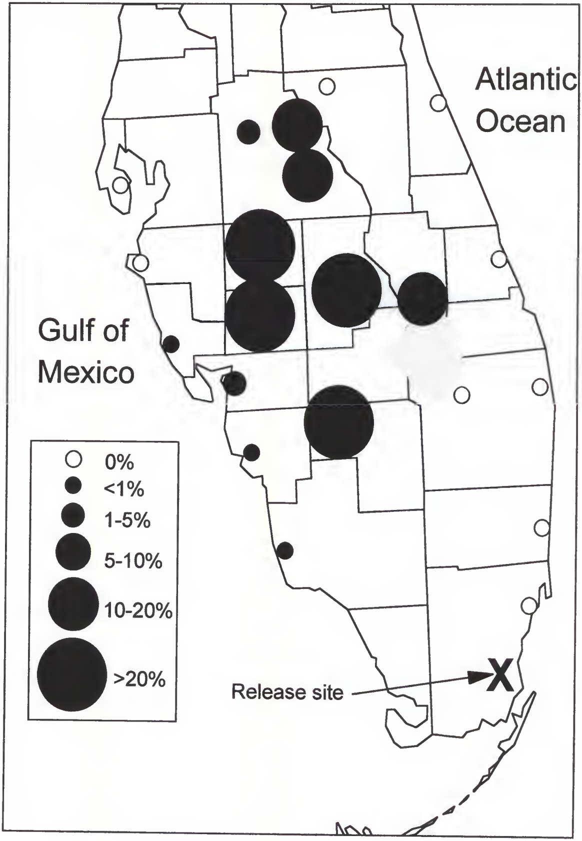

Figure 3-3. Parasitism by *Doryctobracon areolatus* in Surinam cherry.

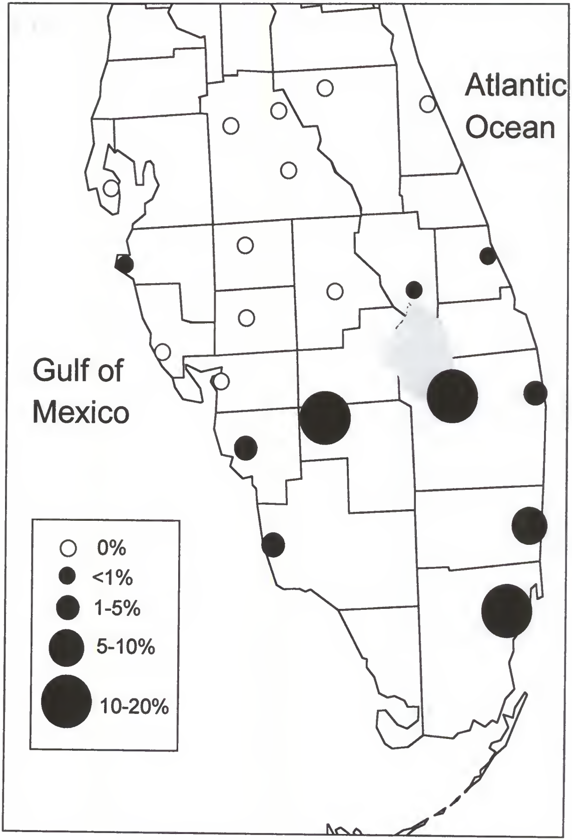

Figure 3-4. Parasitism by *Diachasmimorpha longicaudata* in Surinam cherry.

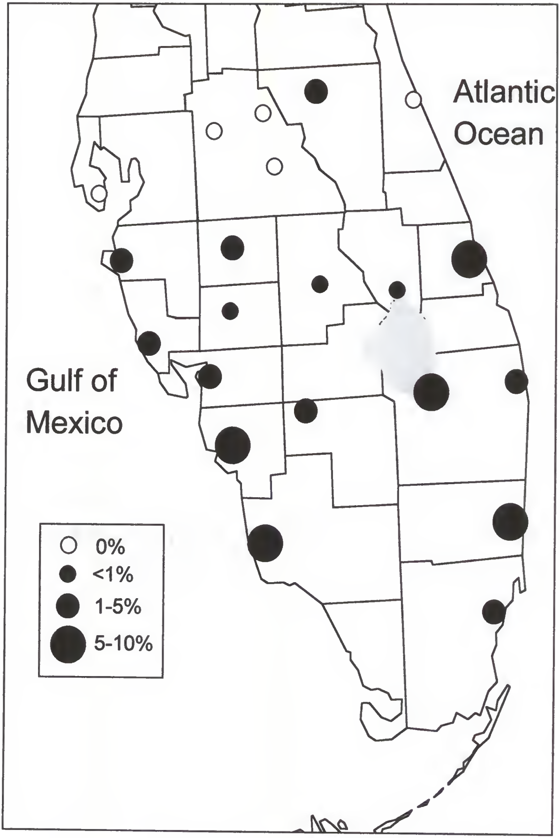

Figure 3-5. Parasitism by *Utetes anastrephae* in Surinam cherry.

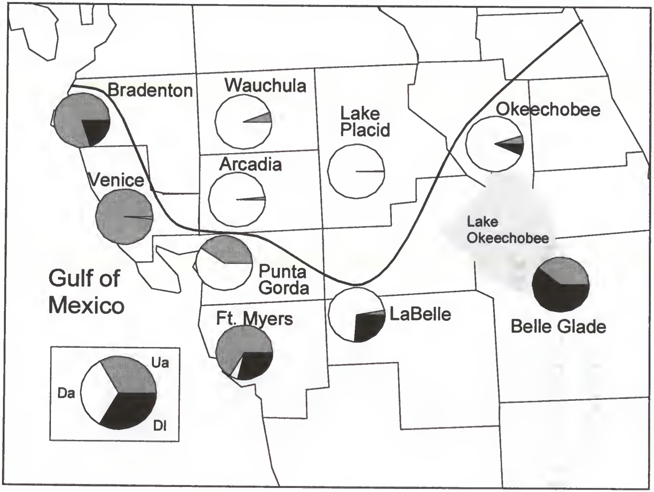

Figure 3-6. Relative abundance of parasitoid species in Surinam cherry in the region of co-occurrence. Da= *Doryctobracon areolatus*; Dl= *Diachasmimorpha longicaudata*; Ua= *Utetes anastrephae*. The solid line represents the northern limit of distribution for *D. longicaudata*.

Table 3-12. Mean host fruit plant density (trees/ km of road) (SE) in various towns.

Town	Loquat	Surinam cherry	Cattley guava	Common guava
Arcadia	3.4 (0.4) cde	2.6 (0.4) ef	0.8 (0.1) bcd	0.10 (0.06) b
Belle Glade	2.2 (0.5) ef	7.7 (0.8) bc	0.2 (0.02) cd	0.5 (0.3) b
Bradenton	3.3 (0.6) cde	4.6 (0.7) cde	0.3 (0.1) cd	0.02 (0.02) b
Dade City	6.5 (0.4) a	0.04 (0.04) f	0 d	0.04 (0.04) b
Ft. Lauderdale	1.8 (0.4) ef	5.3 (0.9) bcde	0.5 (0.2) bcd	0 b
Ft. Myers	0.9 (0.2) f	2.7 (0.3) ef	0.6 (0.1) bcd	0.06 (0.04) b
Ft. Pierce	4.4 (0.5) abcd	4.9 (0.9) cde	1.4 (0.7) b	0.2 (0.1) b
LaBelle	3.0 (0.8) cdef	3.4 (0.8) e	1.0 (0.2) bc	2.4 (0.9) a
Lakeland	3.5 (1.4) cde	3.7 (0.4) e	0 d	0.06 (0.04) b
Lake Placid	2.9 (1.2) cdef	4.9 (0.9) cde	0.5 (0.2) bcd	0.5 (0.3) b
Lake Wales	6.1 (0.6) ab	7.4 (0.8) bcd	0.5 (0.2) bcd	0.4 (0.2) b
Melbourne	5.9 (1.1) ab	3.2 (1.0) ef	0.3 (0.1) cd	0.3 (0.1) b
Miami	1.1 (0.4) f	12.9 (3.9) a	0.3 (0.2) cd	0.7 (0.3) b
Naples	2.5 (0.3) def	4.8 (0.3) cde	3.9 (1.2) a	0.10 (0.06) b
Okeechobee	3.1 (0.2) cdef	3.7 (0.4) e	0.5 (0.1) cd	0.6 (0.3) b
Punta Gorda	3.9 (1.7) bcde	4.2 (1.1) de	0.3 (0.1) cd	0 b
St. Cloud	3.4 (0.6) cde	2.3 (0.6) ef	0.2 (0.1) cd	0.2 (0.1) b
St. Petersburg	3.0 (0.2) cdef	8.2 (2.0) b	0.2 (0.1) cd	0.06 (0.03) b
Tampa	5.8 (1.1) ab	2.6 (0.5) ef	0.2 (0.1) cd	0.04 (0.04) b
Venice	2.4 (0.3) def	2.3 (0.6) ef	0.6 (0.2) bcd	0 b
Wauchula	4.8 (0.6) abc	3.5 (1.0) e	0.8 (0.2) bcd	0.8 (0.2) b

Means within a column followed by the same letter are not significantly different, p=0.05 according to the Waller-Duncan k-ratio t test, and k-ratio=100.

Relationships With Environmental Factors

The northern limit of *D. longicaudata* distribution closely fits the isotherm of 10.5° C January mean minimum temperature (Figure 3-7). The number of frost days also fits the distribution somewhat (see map in Fernald 1981), but to a lesser degree. Mean minimum temperature for the coldest month was not a significant factor in the logistic regression analysis (χ^2=3.51, p=0.061). Rather, presence of this parasitoid was best explained by low variability in monthly temperatures (Table 3-13). Four different variance factors were negatively related with presence of *D. longicaudata*, including variance of extreme maximum, extreme minimum, mean maximum and mean temperature. Other factors significantly related with presence of *D. longicaudata* included mean and extreme minimum temperatures (positive relationships) and abundance of loquat trees (negative relationship). In contrast with *D. longicaudata*, variance of temperatures had a positive relationship with presence of *D. areolatus*. In this case the significant factor associated with parasitoid distribution was variance of extreme minimum temperatures (Table 3-13). Presence of *D. areolatus* was also positively associated with extreme maximum temperatures. Note that summer temperatures are often greater at northern and inland sites than at southern and coastal locations (Table 3-2). Presence of *U. anastrephae* showed no significant relationships with abiotic factors, but was negatively related with abundance of loquat trees.

Density of guava trees was positively related with total parasitism in both loquat and Surinam cherry (Table 3-14). Other factors significantly associated with total parasitism include variance of extreme minimum temperatures (positive relationship in Cattley guava), extreme maximum temperature (positive relationship in common guava)

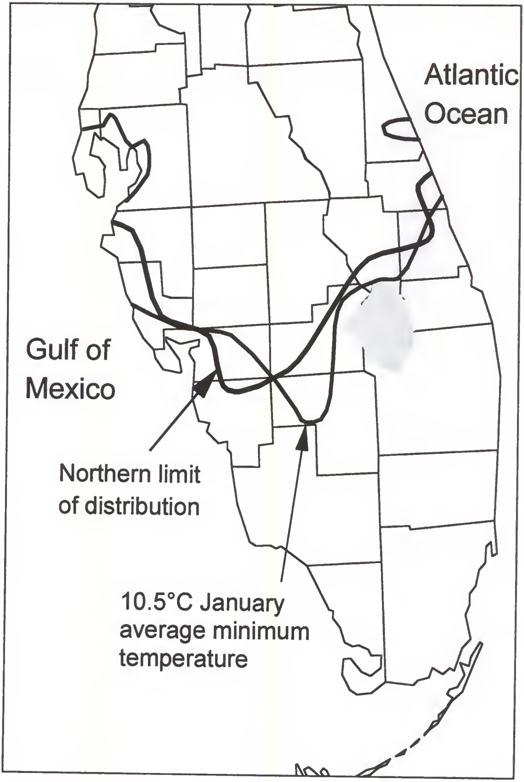

Figure 3-7. Relationship between the northern observed limit of *Diachasmimorpha longicaudata* distribution and January mean minimum temperature.
The isotherm was copied from Fernald (1981), based on data from the years 1960-1979.

and variance of precipitation (positive relationships in loquat and common guava, multiple factor models).

D. areolatus was more common at sites with lower mean temperatures, in both Surinam cherry and Cattley guava (multiple and single factor models, respectively; Table 3-15). Similarly, parasitism levels in common guava were negatively associated with extreme minimum temperatures (multiple factor model). Variance of extreme maximum temperatures was negatively related with *D. longicaudata* abundance in Surinam cherry (multiple factor model). Variance of precipitation was positively associated with *D. areolatus* abundance in Cattley and common guava, and with *D. longicaudata* abundance in loquat (multiple factor models).

Guava tree density was significantly associated with parasitism levels of both *D. areolatus* (positive relationship in Surinam cherry) and *D. longicaudata* (positive relationships in loquat and Surinam cherry, multiple factor models) (Table 3-15). Loquat tree density was negatively related with *D. longicaudata* parasitism levels in Surinam cherry and common guava (multiple factor models). Similarly, Surinam cherry tree density was negatively related with *D. longicaudata* abundance in common guava (multiple factor model). A highly significant positive relationship was observed between Surinam cherry tree density and parasitism levels of *U. anastrephae* in Cattley guava. Interestingly, there were no significant relationships between tree density and parasitism on the same host.

Highly significant positive relationships were found between fly trapping and parasitism by *D. longicaudata* in loquat and common guava (minimum and mean monthly capture of host flies, respectively; Table 3-16). Similar, but less significant,

Table 3-13. Environmental factors significantly associated with presence or absence of parasitoid species, according to logistic regression analysis.

Parasitoid species	Factor (relationship)	p	χ^2
D. areolatus	Var extreme min temp (+)	0.039	4.26
	Extreme max temp (+)	0.045	4.00
D. longicaudata	Var extreme max temp (-)	0.016	5.79
	Var extreme min temp (-)	0.017	5.69
	Var mean max temp (-)	0.028	4.82
	Var mean temp (-)	0.030	4.70
	Mean temp (+)	0.035	4.46
	Extreme min temp (+)	0.038	4.28
	Loquat density (-)	0.039	4.25
U. anastrephae	Loquat density (-)	0.016	5.78

Extreme min temp = Extreme minimum annual temperature.
Extreme max temp = Extreme maximum annual temperature.
Loquat density = Mean density of loquat trees.
Var extreme min temp = Variance of monthly extreme minimum temperatures.
Var extreme max temp = Variance of monthly extreme maximum temperatures.
Var mean temp = Variance of monthly mean temperatures.
Var mean max temp = Variance of monthly mean maximum temperatures.

relationships were observed between minimum capture and abundance of *U. anastrephae* in loquat and Surinam cherry. No significant relationships were found between fly trapping variables and parasitism by *D. areolatus*.

Discussion

Factors possibly affecting parasitoid distribution and abundance can be grouped into three categories: (1) abiotic factors, e.g. temperature and precipitation; (2) host

Table 3-14. Environmental factors significantly associated with parasitism levels of all parasitoid species combined.

Host fruit	Single factor model[a]			Multiple factor model[b]		
	Factor (relationship)	p[c]	r^2	Factors (relationship)	p[c]	r^2
Loquat	Guava density (+)	**	0.34	Guava density (+) Var precipitation (+)	* **	0.61
Surinam cherry	Guava density (+)	***	0.52	-----		
Cattley guava	Var extreme min temp (+)	*	0.36	-----		
Common guava	Extreme max temp (+)	*	0.21	Extreme max temp (+) Var precipitation (+)	* *	0.42

[a]Linear regression with the factor which best explains variation in the data.
[b]Multiple linear regression with factors having significant linear relationships with the relevant parasitism level.
[c]* $p<0.05$; ** $p<0.01$; *** $p<0.001$.
Guava density = Mean density of common guava trees.
Extreme max temp = Extreme annual maximum temperature.
Var extreme min temp = Variance of the monthly extreme minimum temperatures.
Var precipitation = Variance of the monthly precipitation.

availability; and (3) competition with other species. These environmental effects are summarized in Figure 3-8.

The northern limit of *D. longicaudata* distribution is closely related to the January mean minimum isotherm of 10.5°C, as derived from Fernald (1981). This suggests that winter temperatures limit the distribution of this species. This could be an important factor affecting tropical parasitoid species in warm temperate localities. Snowball and Lukin (1964) suggested that winter temperatures may limit the establishment of *Fopius arisanus* in Australia.

Sivinski et al. (1998) reported a reduction in winter in the abundance of *D. longicaudata* relative to that of *D. areolatus* in calamundin at LaBelle. This suggests

Table 3-15. Environmental factors significantly associated with parasitism levels of the various parasitoid species, for towns in which the relevant parasitoid was collected.

Species[a]	Host fruit	Single factor model[b]			Multiple factor model[c]		
		Factor (relationship)	p[d]	r^2	Factors (relationship)	p[d]	r^2
Da	Loquat	-----			-----		
	Surinam cherry	Guava density (+)	*	0.50	Guava density (+) Mean temp (-)	** **	0.81
	Cattley guava	Mean temp (-)	**	0.90	Mean temp (-) Var precipitation (+)	*** *	0.98
	Common guava	-----			Extreme min temp (-) Var precipitation (+)	*** **	0.84
Dl	Loquat	-----			Guava density (+) Var precipitation (+)	* *	0.68
	Surinam cherry	-----			Var extreme max temp (-) Guava density (+) Loquat density (-)	** *** **	0.87
	Cattley guava	-----			-----		
	Common guava	-----			Loquat density (-) Sur cherry density (-)	* *	0.75
Ua	Loquat	-----			-----		
	Surinam cherry	-----			-----		
	Cattley guava	Sur cherry density (+)	**	0.68	-----		

[a]Da = *Doryctobracon areolatus*; D l= *Diachasmimorpha longicaudata*; Ua = *Utetes anastrephae.*
[b]Linear regression with the factor which best explains variation in the data.
[c]Multiple linear regression with factors having significant linear relationships with the relevant parasitism level.
[d]* $p<0.05$; ** $p<0.01$; *** $p<0.001$.
Sur cherry density = Mean density of Surinam cherry trees.
Guava density = Mean density of common guava trees.
Loquat density = Mean density of loquat trees.
Extreme min temp = Extreme annual minimum temperature.
Mean temp = Mean annual temperature.
Var extreme max temp = Variance of the monthly extreme maximum temperatures.
Var precipitation = Variance of the monthly precipitation

Table 3-16. Fly trapping variables significantly associated with mean parasitism levels.

Parasitoid	Host fruit	Variable (relationship)[a]	p[b]	r^2
D. longicaudata	Loquat	Minimum (+)	***	0.64
	Common guava	Mean (+)	***	0.68
U. anastrephae	Loquat	Minimum (+)	**	0.38
	Surinam cherry	Minimum (+)	*	0.30

[a]Linear regression with the factor which best explains variation in the data.
Mean = Mean monthly capture (flies/trap).
Minimum = Minimum monthly capture (flies/trap).
[b]* $p<0.05$; ** $p<0.01$; *** $p<0.001$.

some climatic effect unrelated to host availability. A similar conclusion was reached by Snowball (1966) regarding abundance of *F. arisanus* in southern Australia. Laboratory studies suggest that *D. longicaudata* may be less tolerant to low temperatures than its host *A. suspensa* (Chapter 5). Further studies are needed to determine whether its tolerance is lower than that of *D. areolatus*.

Note that mean minimum temperature was not a significant factor in the logistic regression analysis. Rather, absence of *D. longicaudata* was best explained by high variability in temperatures (Table 3-13). The possible significance of this observation is discussed below.

Parasitoid populations interact with the temporal and spatial distribution of their hosts, and the dynamics of both host fruits and fly populations may be important. The three towns from which parasitoids were not collected all have some type of low host availability. At Dade City, the most northern town in this study, all host plants except loquat are absent or rare (Table 3-12). Thus, hosts are available for only a short period of time in early spring. Note that host larvae are not uncommon in loquat at Dade City, with

91% of samples collected producing flies (Table 3-4). Host fly densities in Brevard county (Melbourne) are among the lowest of all counties included in this study (Table 3-3). Only 63% of samples collected at Melbourne produced flies (Table 3-4). Hosts are also relatively rare in Pinellas county (St. Petersburg) (Table 3-3), with only 68% of samples collected producing flies (Table 3-4). Note also that Pinellas county is a peninsula, separated form the east and south by Tampa Bay. This body of water may be an ecological barrier to parasitoids, making colonization difficult.

Fluctuations in fruit availability would depend primarily on abiotic conditions including temperature and precipitation (Petr 1991, Raper and Kramer 1983). High variability in temperatures could lead to greater heterogeneity in the temporal occurrence of fruit. Thus the negative relationships between the variances of several temperature variables and occurrence of *D. longicaudata* (Table 3-13) may indicate that this parasitoid is dependent on a relatively constant supply of hosts. This hypothesis is supported by the highly significant relationship between numbers of flies trapped and parasitism by this species in loquat and guava (Table 3-16).

Spatial distribution of host fruits is dependent upon (1) the number of fruits per tree and (2) the number of trees per unit area. The number of fruits per tree depends on various factors including tree size and age, degree of shading, and horticultural practices such as pruning, watering and fertilization. Although these factors may vary among towns, no data on this are available.

In several cases, parasitism appears to be related to host tree density. Guava tree density accounts for 34 and 52% of the variation in total parasitism for loquat and Surinam cherry, respectively (Table 3-14). It is a significant factor in the abundance of

both *D. areolatus* and *D. longicaudata* (Table 3-15). Guava is usually the last available major host before the onset of winter. Thus its abundance may be an important determinant of the size of the overwintering population, which in turn affects the abundance of parasitoids in loquat and Surinam cherry the following spring.

In Hawaii, *D. longicaudata* is more common in orchards than in wild guava (Vargas et al. 1993). The authors suggest that two possible factors contributing to this observation may be high tree densities and abundance of rotting fruit in commercial guava orchards.

The density of Surinam cherry trees accounts for 68% of the variation in *U. anastrephae* abundance in Cattley guava (Table 3-15). This result is expected because Surinam cherry is the major host for *U. anastrephae* (Table 3-6), and it immediately precedes Cattley guava in fruiting. Note, however, that *U. anastrephae* was recovered from Cattley guava in three towns only (Table 3-10), and a regression analysis based on three points should be treated with caution.

Significant negative relationships between fruit tree density and parasitism are probably artifacts. The absence of *U. anastrephae* in towns with high incidence of loquats may reflect a tendency of loquats to survive in towns that have an unsuitable climate for other tropical fruits, and that the lack of the latter is what actually accounts for the absence of parasitoids (loquats flourish and fruit well north of the normal range of *A. suspensa*, pers. obs.). Dade City, Melbourne and Tampa, among the towns with the highest loquat densities, all have relatively low densities of other host fruits (Table 3-12).

When all towns except LaBelle are considered, abundance of *D. areolatus* is negatively related to that *D. longicaudata* (Figures 3-3, 3-4 and 3-6). *Diachasmimorpha*

longicaudata and *D. areolatus* are of similar size, and both have long ovipositors (Sivinski et al. 1997). They also show similar preferences to the host fruits (Table 3-6), and attack the same stage larvae (Lawrence et al. 1976, Chapter 6). Thus the potential for competition between these species is obvious. Note that the interaction between them is a new association, as *D. areolatus* is a neotropical species, while *D. longicaudata* originates in the Indo-Pacific region (Clausen 1978). Therefore, they would not have evolved niche divergence to avoid competition.

D. areolatus was established in large numbers after being introduced to southern Florida (Baranowski and Swanson 1970), but has subsequently diminished and possibly disappeared from the region of its introduction. The current distribution pattern suggests that competition by *D. longicaudata* may have caused its displacement. Note that *D. longicaudata* was introduced three years following the introduction of *D. areolatus*. Thus *D. areolatus* had time to become established and migrate to favorable locations to the north prior to the establishment of *D. longicaudata*. It is intriguing to think that had the sequence of introductions been reversed, *D. areolatus* may not have successfully been established.

Similar cases involving fruit fly parasitoids in Hawaii are considered among the classic examples of apparent competitive displacement. *Psyttalia* (*Opius*) *humilus* (Silvestri) was the dominant parasitoid of the *C. capitata* in 1915, and was replaced by *Diachasmimorpha tryoni* (Cameron) from 1916 onward (Pemberton and Willard 1918). This displacement was apparently due to competitive superiority of the first-instar larvae of the latter species. During the late 1940s, several parasitoid species were released for the control of *B. dorsalis* (Clausen et al. 1965). Initially, *D. longicaudata* was the

dominant species, only to be replaced by *Fopius (Biosteres) vandenboschi* (Fullaway), which was in turn replaced by *Fopius (Biosteres) arisanus* (Sonan) (van den Bosch et al. 1951). Two contributing mechanisms were offered for this displacement. First, the displacing species attack progressively earlier immature stages, which would be more prone to parasitism because of their proximity to the fruit surface. Second, *F. arisanus* larvae appeared to inhibit the development of the other species, while *F. vandenboschi* larvae also inhibit development of *D. longicaudata* (van den Bosch and Haramoto 1953).

In contrast to the report of van den Bosch and Haramoto (1953), several studies indicate that *D. longicaudata* may have a competitive advantage over other parasitoid species in situations of multiparasitism. Palacio et al. (1991) found that *D. longicaudata* was a superior competitor to both *F. arisanus* and *Fopius (Biosteres) persulcatus* Silvestri, indicating physical competition among first-instar larvae. Ramadan et al. (1984) suggested a similar advantage of *D. longicaudata* over *D. tryoni* in *C. capitata* hosts. Studies by Bautista and Harris (1997) with *D. longicaudata* and *Psyttalia incisi* (Silvestri) indicate that the sequence of oviposition is important, with the first parasitoid species to which the host is exposed having an advantage. However, while exposure first to *P. incisi* resulted in 77% of the progeny being of this species, the reverse sequence resulted in 99% of the progeny being *D. longicaudata*. These studies support the possibility that *D. longicaudata* may be a superior competitor to *D. areolatus* in multiparasitized hosts.

To summarize, the two major phenomena observed in this study are the absence of *D. longicaudata* in the interior region of central Florida, and the absence of *D. areolatus* in portions of southern Florida. Which factors may affect the interactions

between *D. areolatus* and *D. longicaudata*, and how could this result in the observed pattern of distribution? Sivinski et al. (1998) hypothesized that the co-occurrence of both species at LaBelle may be the result of "counter-balanced competition" (cf. Zwölfer 1971) where *D. areolatus* is superior to *D. longicaudata* in locating host patches (=extrinsic competitor) and *D. longicaudata* is superior in exploiting these patches (=intrinsic competitor). The better searcher would be at an advantage at locations that have a less predictable supply of hosts in time or space, while the better intrinsic competitor would benefit from more homogeneous host availability. In the more northern interior regions of Florida, where temperatures are more variable, large gaps may occur between fruiting cycles of the various hosts, and in particular between the fall fruiting of guava and the spring fruiting of loquat. At coastal locations where temperature conditions are more homogeneous, trees may have more than one fruiting cycle, filling in the temporal gaps in fruit availability (Nguyen et al. 1992). Furthermore, additional tropical host fruits occur in the southern coastal regions (see Hennessey 1994). The former conditions would favor the superior searcher, presumably *D. areolatus*, while the latter would benefit the superior intrinsic competitor, i.e., *D. longicaudata*. In extreme conditions one parasitoid species may driven to extinction, and at intermediate locations both would persist. At LaBelle large temporal gaps in hosts may be balanced by spatial abundance, in particular of guava, enabling the persistence of a sizable population of *D. longicaudata*.

Diapause development is an important mechanism allowing insects to cope with periods of low host availability. There is evidence that *D. longicaudata* individuals do indeed enter diapause (Aluja et al. submitted, Ashley et al. 1976, Clausen et al. 1965,

Chapter 5). However, in Mexican populations both the proportion of individuals entering diapause and the length of diapause period are greater for *D. areolatus* than for *D. longicaudata* (Aluja et al. submitted). Additionally, Aluja et al. (submitted) report circumstantial evidence that *D. areolatus* adults may enter a reproductive diapause. These observations suggest that *D. areolatus* populations may be able to better survive long periods without hosts.

The presumed competitive advantage of *D. longicaudata* over *D. areolatus* may be the result of other mechanisms, besides larval competition. *Diachasmimorpha longicaudata* may have an advantage in locating fruits containing host larvae, or in locating larvae within fruits. *Diachasmimorpha longicaudata* locates hosts within fruits by sensing the vibrations of the feeding larvae (Lawrence 1981). In the laboratory *D. longicaudata* females can locate hosts without the presence of host fruit odors. On the other hand, host larvae alone are not attractive to *D. areolatus* females, and addition of fresh fruit odors is sufficient to stimulate oviposition behavior in this species (Chapter 7). It is possible that *D. areolatus* may respond to host vibrations following exposure to host fruit odors. However, its dependence on fruit odors suggests that vibrations may be a relatively less important stimulus for *D. areolatus* than for *D. longicaudata*, and consequently it may be at a disadvantage in locating larvae within fruit. Conversely, this dependence on fruit odors may indicate a superior ability of *D. areolatus* to locate host patches. Note, however, that *D. longicaudata* females are attracted to volatiles associated with rotting fruit (Greany et al. 1997).

Additionally, *D. longicaudata* would have a competitive advantage if it were more fecund. In the laboratory, *D. longicaudata* can produce a large number of progeny

over a short period of time, with most eggs laid within a few days (Greany et al. 1976). On the other hand, *D. areolatus* appears to produce smaller numbers of progeny over longer periods of time (Chapter 6). If this is the case in the field, an individual *D. longicaudata* female, after locating the host patch, could exploit it at a faster rate than a *D. areolatus* female.

Finally, the ovipositor of *D. longicaudata* is longer than that of *D. areolatus* (*D. longicaudata*, 5.49 ± 0.21 mm, range 4.67-6.40 mm, n=7; *D. areolatus*, 3.80 ± 0.11 mm, range 3.43-4.11 mm, n=7; t=7.18, p<0.0001). The ovipositor of *D. longicaudata* is also consistently longer in relationship to body size as estimated by the ratio between ovipositor length and wing length (t=14.59, p<0.0001, n=7). This enables *D. longicaudata* to reach larvae deeper within fruits, thus allowing access to a larger proportion of larvae, especially in large fruits (Sivinski et al. 1997).

As discussed above, *D. longicaudata* distribution may be limited to the north by (1) direct effects of low winter temperatures or (2) periods of low host availability. There is some evidence in support of both hypotheses. The two effects could act in concert, and may not be mutually exclusive.

Some support for the second hypothesis can be found in the literature. Preliminary observations in Mexico, suggest that *D. longicaudata* is less common at low altitudes (M. Aluja, pers. comm.). This is the opposite of what would be expected if this species was adversely affected by low temperatures. The low altitude habitats are drier, and as a result there are larger gaps in host availability. Thus, the temporal availability of hosts at low altitudes in Mexico is similar to that in the colder regions of Florida.

In Mexico, *D. longicaudata* is the dominant species in an area of mixed cultivation, while it is absent in native habitats where *D. areolatus* is most common (Aluja et al. 1990, Hernandez-Ortiz et al. 1994). Similarly, in Amazonas State, Brazil, *D. areolatus* is the dominant parasitoid in rural locations while *Opius* sp. nr. *bellus* is dominant in urban areas (Canal D. et al. 1995). Native habitat is more heterogeneous in host availability, favoring a superior searcher, while there is a more predictable supply of hosts in cultivated or urban areas, which would favor the better intrinsic competitor. In both cases, the presence of wild hosts may give *D. areolatus* refuge from competition, thus preventing displacement. Such a refuge does not exist in Florida, where most hosts are in either urban or agricultural habitats. Feral populations of guavas exist in some areas, but fruiting of these trees is mostly limited to late summer.

The biology of *U. anastrephae* is little known, and its interactions with other parasitoid species unclear. Laboratory rearing data from Brazil suggest that it attacks the same larval instars as *D. areolatus* and *D. longicaudata* (R. Sugayama, pers. comm.). In Mexico, Sivinski et al. (1997) observed negative relationships between *U. anastrephae* and *D. areolatus* within tree canopies. This was interpreted as being the possible result of evolution of divergent niches in these sympatric species, which would reduce direct competition. However, the inverse among-site relationship observed between these two species in this study suggests that significant within-site competition may be occurring. Note that *U. anastrephae* is common only in small fruits such as Surinam cherry (Table 3-6). Thus significant competition would only occur in such fruits. As *D. areolatus* was established in Florida with *U. anastrephae* already present, in appears that competition by *U. anastrephae* alone is not highly significant. However, *U. anastrephae* occurs in large

numbers in most of the same towns where *D. longicaudata* is common (Figures 3-4 through 3-6). Thus, coupled with the competitive pressure of *D. longicaudata*, it may have contributed to the displacement of *D. areolatus*. Alternatively, *U. anastrephae* may be common at these locations because *D. longicaudata* had suppressed *D. areolatus*, thus releasing the former species from competition.

There has been some debate over the merits of multiple introductions of natural enemies in biological control programs. Some workers have suggested that interspecific competition may reduce the overall level of host suppression, while others claim that additional species would increase control levels (see discussion in Van Driesche and Bellows 1996). DeBach and Rosen (1991) state that "displacement of a fairly effective established natural enemy species by another imported species means that the second one is more effective, and will produce even better host population regulation". Could the displacement of *D. areolatus* by *D. longicaudata* have reduced the suppression of the Caribbean fruit fly? This scenario appears to be possible. Mean parasitism levels for *D. areolatus* in Surinam cherry surpassed 20% at four towns, and at LaBelle reached 36% (Table 3-9). Meanwhile, mean parasitism for *D. longicaudata* was no higher than 15% (at Miami). Even with *D. longicaudata* and *U. anastrephae* combined, the highest mean parasitism level was 20% (at Belle Glade). Thus it appears that *D. areolatus* may be able to contribute to higher levels of control than the other parasitoid species, possibly due to its greater searching efficiency.

If this is the case, how then could this more efficient parasitoid be displaced? We could attempt to understand parasitoid population dynamics on a regional scale by examining the possible dynamics within individual host trees. Consider two Surinam

cherry trees. The first produces large numbers of fruits over a short period of time. Host larvae would be abundant, and parasitoids would be limited by the number of fruits and larvae that they could locate. As more individuals of the superior searcher would be able to locate the resource quickly, on a population level it would be capable of locating greater numbers of larvae. The second tree produces fruits over a long period of time in limited patches. The superior searcher would have the initial advantage of colonizing the resource more quickly. However, after the superior intrinsic competitor finally locates the resource, the latter species would have the advantage. While over time the former species may parasitize on average a higher proportion of hosts, towards the end of the fruiting cycle the latter species would dominate and possibly displace the superior searcher. Such dynamics (though not leading to displacement) where observed within trees at LaBelle, with both the relative and absolute numbers of *D. longicaudata* increasing over time (Sivinski et al. 1998). Note that parasitism by *D. longicaudata* can approach 100% at the end of the fruiting period in fruits such as Surinam cherry. If the majority of host trees within a town were of the second type, total displacement could occur. Fruiting patterns within trees are dependent on weather conditions, and could change over time. It is conceivable that in certain years most trees would be of the second type, and the population dynamics would lead to displacement. In other years the first type may dominate, and if displacement had previously occurred, the remaining parasitoid would not sufficiently respond to the growing host population, and parasitism levels would be low. In conclusion, a superior intrinsic competitor may displace a superior searcher, leading to a reduction in host suppression.

D. areolatus is absent or rare at northern coastal locations, even though total parasitism at these sites is low. It appears that other factors besides competition must account for this absence. This suggests that unidentified environmental factors associated with coastal locations may have contributed to its disappearance from southern Florida as well. However, if coastal conditions were unsuitable to *D. areolatus*, it would not have been expected to become established in large enough numbers to enable it to spread to distant regions of the state. Perhaps widespread pesticide applications against mosquitoes and other biting insects, which is most prevalent in coastal regions, contributed to its disappearance.

Could *D. areolatus* have displaced *D. longicaudata* in central Florida, just as *D. longicaudata* may have displaced *D. areolatus* in the south? *D. areolatus* obviously migrated from its original release area in southern Florida to the areas in which it currently dominates in the central part of the state. However, it is unclear whether it was present there when *D. longicaudata* was released in 1972, only three years after its own introduction. Could a superior searcher displace a superior intrinsic competitor? Although a superior searcher would have a relative advantage in a situation of less predictable hosts, allowing it to be more successful on a population level, the superior competitor by definition would have an advantage when both species occur together on a patch, regardless of the mechanism of competition. It is more likely that the superior competitor would be driven to extinction due to lack of hosts than because of effects of a less competitive parasitoid species.

Is it advisable to release *D. longicaudata* in periodic inundative releases in the regions of central Florida from which it is presently absent? It is quite easy to rear *D.*

longicaudata in the laboratory, and mass-rearing can be achieved at relatively low cost. In contrast, *D. areolatus* is much more difficult to rear (Chapter 6). Therefore, it would be cost-effective if the program of inundative releases of *D. longicaudata* could be expanded to all regions of Florida (see Burns et al. 1996). There is evidence that large-scale inundative releases of *D. longicaudata* could reduce host populations (Sivinski et al. 1996). The numbers of parasitoids released is presumably much higher than those naturally occurring in the field (Knipling 1992). Thus, there is no real difference between augmenting existing populations and releases in areas where parasitoids do not occur. There is no reason to believe the parasitoids would not be as effective in all regions of the state, at least during warm periods of the year. However, there is a substantial risk that these releases would cause the permanent displacement of *D. areolatus*. If releases are terminated after such a displacement, *D. longicaudata* would not be expected to become permanently established (because they would not survive the winter or periods lacking in hosts), and no parasitoids would remain. Thus initiation and subsequent termination of an inundative release program for *D. longicaudata* could ultimately lead to an explosion of *A. suspensa* populations. If inundative parasitoid release in central Florida is pursued, it may be more advisable to develop more cost-effective rearing procedures for *D. areolatus*, with the objective of releasing this species in areas where it currently occurs.

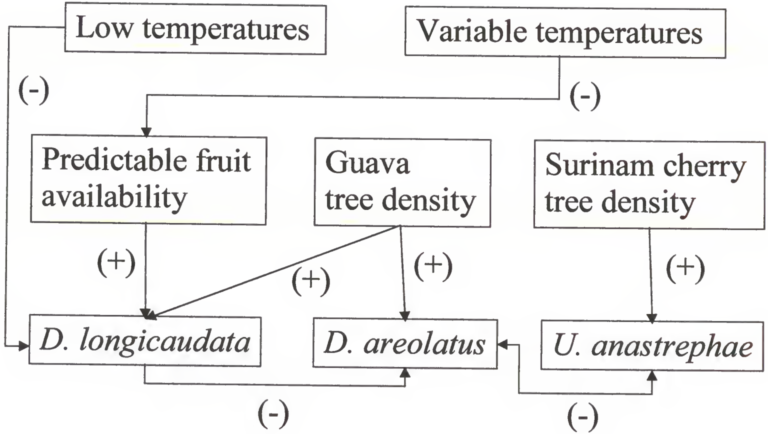

Figure 3-8. Summary of factors possibly affecting parasitoid abundance.

CHAPTER 4
LOCAL TEMPORAL AND SPATIAL DISTRIBUTION PATTERNS OF *DIACHASMIMORPHA LONGICAUDATA* AND *DORYCTOBRACON AREOLATUS* IN AN AREA OF CO-OCCURRENCE

The distributions of *Diachasmimorpha longicaudata* and *Doryctobracon areolatus* overlap in Florida only within a limited region (Chapter 3). The town of LaBelle, situated between Lake Okeechobee and the Gulf of Mexico, is one of the few locations in which both are common (Chapter 3, Sivinski et al. 1996, 1998). Studies of the temporal and spatial dynamics of these parasitoids at LaBelle may help explain how they co-occur at this location, while in most areas of Florida they do not. More specifically, they could address hypotheses generated in Chapter 3, i.e. that low temperatures have a direct or indirect negative effect on *D. longicaudata*, and that interspecific competition could partially explain the disappearance of *D. areolatus* from southeastern Florida.

Temporal and spatial dynamics of these species within trees were studied by Sivinski et al. (1998, pers. comm.). This chapter examines similar dynamics on a larger scale, by comparing parasitoid abundance among trees within LaBelle. Additionally, I examined the temporal dynamics of the population as a whole, both within and among years.

Materials and Methods

Fruit Sampling in 1996

Loquat (*Eriobotrya japonica* (Thunb.)) and Surinam cherry (*Eugenia uniflora* L.) fruits were sampled at LaBelle and the adjacent town of Ft. DeNaud every two weeks from Week 4 (late January) to Week 22 (early June) of 1996. Most loquats were sampled from Week 4 to Week 14, but some were available until Week 18. Most Surinam cherries were sampled from Week 14 to Week 22, with one sample each collected in Weeks 4 and 6. Every tree within the towns which was found to have at least ten fruits was sampled. Each sample included fruits from a single tree. A total of 256 samples was collected, ranging from 3 in Week 4 to 51 in Week 16. Numbers of fruits per sample ranged between 17-106 for loquat, and between 18-151 for Surinam cherry. These numbers represented either all fruits present on the tree, or the maximal number that could be put in a single layer on the screen within the bucket (see Chapter 3 for details of fruit handling after collection). Fruits were sampled randomly from different parts of the tree. Each fruit sample was weighed following collection. Upon intensive collection of Surinam cherry fruits, it became apparent that they were infested by large numbers of fungal spores. Therefore, beginning in Week 18, fruits were washed in a 0.03% solution of sodium benzoate.

Abundance of the three parasitoid species, *D. areolatus*, *D. longicaudata* and *Utetes anastrephae*, was compared between LaBelle and Ft. DeNaud. Due to significant differences between the two towns (see Table 4-1), all subsequent analyses included only

data from LaBelle. Additionally, because *U. anastrephae* was relatively uncommon at LaBelle, in was not considered in these analyses.

Analysis of Distribution Among Trees

Spatial distributions of Caribbean fruit flies, *Anastrepha suspensa* (Loew), and their parasitoids among trees were examined using data collected in LaBelle during 1996. Distribution was visualized using the Surfer software program (Golden Software) and the kriging method. Kriging uses sampled data to produce a grid of estimated values quantifying the entire distribution of the parameter of interest. Ultimately, kriged data are used to create isolines of equal parameter density visualized as a 2-dimensional contour map. For a detailed description of spatial analysis and its use in entomology see Brenner et al. (1998). Longitude and latitude coordinates for each host tree were obtained using the Microsoft Automap Street Plus software program, and adjusted slightly to fit a TIGER/Line base map (U.S. Census Bureau).

Figure 4-1 illustrates the quadrants which are included in this analysis. The town of LaBelle, situated to the south of the Caloosahatchee River, can be divided into four quadrants by State Road 80 transecting from east to west, and by State Road 29 running from north to south. A fifth section is in the town of North LaBelle, to the north of the river. Several samples collected in other quadrants were not included in this analysis.

Because of the low occurrence of parasitoids in loquat, only Surinam cherry samples were considered in the spatial analysis. Separate maps were produced for each sampling period, from Week 14 to Week 22. Relationships within each sampling period between fly abundance and that of each parasitoid species, and between parasitoid species, were examined using regression or correlation analysis.

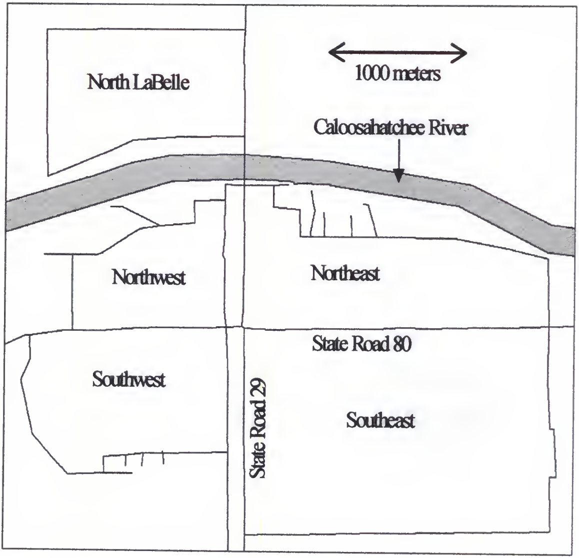

Figure 4-1. Map of LaBelle, Florida, showing quadrants sampled in study.

Temperature Measurements

Parasitoid abundance may be influenced by local variability in temperatures. In order to assess the occurrence of spatial variability in winter temperatures, five Optic StowAway data loggers (Onset Computer Corp.) were placed from December 1996 through March 1997, three at LaBelle and two at Ft. DeNaud. Loggers were placed one meter above the ground on the northern side of major limbs of large Surinam cherry trees, from which a significant number of parasitoids had been recovered during the previous spring. Loggers were set to record the temperature every 24 minutes. Mean, mean minimum and mean maximum temperatures were calculated for each month. These variables were subjected to Friedman's two-way analysis for block designs. This was achieved with the SAS software program by obtaining ranking among sites within days and then performing an analysis of variance on these ranks among sites (SAS Institute 1982). Means were subsequently compared with the Waller-Duncan k-ratio t test. In addition to the above mentioned variables, extreme minimum and maximum temperatures were noted.

Comparisons of Parasitoid Abundance Among Years

Various studies on parasitoids of *A. suspensa* have been conducted at LaBelle during recent years. In addition to data from the current study from 1995 (see Chapter 3) and 1996, Sivinski et al. (1996, 1998) sampled parasitoids for various purposes during each of the years 1991 through 1994. Thus, comparisons of parasitoid abundance among years could be made, and relationships with environmental factors examined.

In 1991 and 1992, samples were collected in a fashion similar to the present study; No more than one sample was collected from each tree in a single week. No manipulations (besides transformation) were performed on these data prior to analysis.

In 1994, multiple samples were collected from each tree in a single day, and often trees were sampled more than once a week. In order to make reliable comparisons with other years, these data were manipulated in the following manner. Samples collected from a single tree on a single day were combined by summing the numbers of parasitoids and flies emerging. Parasitism levels were calculated for each tree each day. Where trees were sampled more than once a week, mean parasitism per tree per week was calculated, and was considered to be a single sample for analysis.

In 1993, two separate studies were performed, one as in 1991-1992 (single sample per tree per week) and the other as in 1994 (multiple samples per tree). Where multiple samples were collected, data were manipulated as with the 1994 data. The resulting parasitism levels per tree per week were considered single samples, and given equal weight in the analysis as samples from the other study.

Note that, as mentioned above, only samples from LaBelle were considered. Thus, the 1995 data used in this chapter is a subset of the "LaBelle" data given in Chapter 3, which includes Ft. DeNaud.

Associations of parasitoid abundance with environmental factors were examined by linear regression analysis. Temperature and precipitation data were obtained from the Southeast Regional Climate Center, Columbia, South Carolina. Parasitism by each parasitoid species in loquat or Surinam cherry was related with the following variables: mean temperature, mean and extreme minimum temperatures, mean and extreme

maximum temperatures, and precipitation. Separate analyses were performed for conditions prevalent during each month preceding fruit collection. Thus, parasitism in loquat was related with temperature and precipitation variables for the months October through February, and parasitism in Surinam cherry was related with these variables for the months October through April.

Results

Comparison of Abundance Between LaBelle and Ft. DeNaud

The various parasitoid species varied greatly in their abundance between LaBelle and Ft. DeNaud during 1996 (Table 4-1). Parasitism by *D. areolatus* in loquat averaged 3% at LaBelle, but it was not collected at Ft. DeNaud. More *D. longicaudata* were recovered from loquat at Ft. DeNaud than at LaBelle, but the difference was not significant. *U. anastrephae* was uncommon in loquat at both towns. The differences between the towns were pronounced in Surinam cherry; *D. areolatus* was more common at LaBelle than at Ft. DeNaud, while both *D. longicaudata* and *U. anastrephae* were more abundant at Ft. DeNaud than at LaBelle. Note that these towns border each other, and the eastern most sample included in this study from Ft. DeNaud is only 2.2 km away from the western most sample from LaBelle. Because of these differences between the towns, only data from LaBelle were included in subsequent analyses.

Table 4-1. Comparisons of percent parasitism by various parasitoid species in 1996 between the towns of LaBelle and Ft. DeNaud.

Fruit	Parasitoid species	LaBelle		Ft. DeNaud		t	p
		n	Mean (SE)	n	Mean (SE)		
Loquat	*D. areolatus*	50	2.87 (1.02)	29	0	3.58	0.001
	D. longicaudata	50	0.09 (0.07)	29	0.61 (0.37)	-1.43	0.16
	U. anastrephae	50	0.02 (0.02)	29	0.03 (0.03)	-0.30	0.77
Surinam cherry	*D. areolatus*	117	30.15 (3.02)	20	5.87 (3.51)	5.12	0.001
	D. longicaudata	117	1.86 (0.49)	20	11.18 (3.57)	-3.02	0.007
	U. anastrephae	117	0.21 (0.09)	20	3.66 (1.52)	-2.41	0.026

Distribution Among Trees

Densities of *A. suspensa* were generally low at the beginning of the Surinam cherry season. During Week 14, flies were concentrated at two focal points, one in the northeastern quadrant of LaBelle, and the second in North LaBelle, just north of the Caloosahatchee River (Figure 4-2). During Week 16, fly densities were again high at these locations. However, high infestations were observed also just to the south of the river, in the southern region of the northwestern quadrant, and at the southern fringes of town (Figure 4-3). Infestation levels were generally higher during Week 18, with highest numbers observed in North LaBelle, the northeastern quadrant just south of the river, and the northwestern quadrant (Figure 4-4). During Week 20, fly numbers were high at most locations, with highest infestations observed in the southwestern quadrant (Figure 4-5). A similar pattern was observed during Week 22, with focal points in the southwestern and northwestern quadrants (Figure 4-6).

D. areolatus was uncommon at the beginning of the Surinam cherry season. During Week 14, only small numbers were recovered from two host trees (Figure 4-7). Note that these were the same trees which had the highest infestations of *A. suspensa* (Figure 4-2). By Week 16, *D. areolatus* was recovered from 11 of 35 host trees. Four focal points were observed, in the northwestern, northeastern and southwestern quadrants (Figure 4-8). Parasitism levels increased dramatically by Week 18, with highest levels (over 50%) observed in the general vicinity of the focal points in the previous sampling period (Figure 4-9). Parasitism of over 50% was widespread during week 20, reaching over 80% in three areas: North LaBelle, the northeastern and extreme northwestern quadrants, and the southwestern quadrant (Figure 4-10). A similar pattern of generally high parasitism levels was observed during Week 22 (Figure 4-11).

D. longicaudata was not recovered from Surinam cherry at LaBelle until Week 16, when it was found in a single host tree just south of the river (Figure 4-12). During Week 18 it was recovered from the same tree, and one additional tree in the southwestern quadrant (Figure 4-13). Parasitism increased dramatically by Week 20, when it was recovered from 11 of 28 hosts. Four focal points with over 10% parasitism were apparent, two each in the northwestern and southwestern quadrants (Figure 4-14). During Week 22, highest parasitism levels were observed in the southwestern quadrant, with a second area of parasitism apparent on both sides of the Caloosahatchee River (Figure 4-15).

Parasitism by *D. areolatus* was significantly related with *A. suspensa* infestation levels during Week 14 (R^2=0.68, F=10.86, p=0.02) and Week 16 (R^2=0.45, F=23.67, p<0.0001), but not Week 18 (R^2=0.11, F=2.73, p=0.11), Week 20 (R^2=0.07, F=1.95, p=0.17), or Week 22 (R^2=0.02, F=0.19, p=0.67). Parasitism by *D. longicaudata* was not

significantly related with *A. suspensa* infestation levels during any week (Week 20, R^2=0.03, F=0.91, p=0.35; Week 22, R^2= 0.10, F=1.09, p=0.32).

The ratio between parasitism by *D. longicaudata* and that by *D. areolatus* mirrors the parasitism by *D. longicaudata* alone during Weeks 20 and 22 (Figures 4-16 and 4-17, compare with Figures 4-14 and 4-15). This is probably due to the relatively even distribution of *D. areolatus* during these weeks (Figures 4-10 and 4-11). Parasitism by the two species was significantly correlated during Week 18 (R=0.44, p<0.03). With all samples considered, there were no significant relationships between parasitism levels of *D. areolatus* and *D. longicaudata* during any other week (Week 16, R=0.10, p=0.60; Week 20, R=0.03, p=0.87; Week 22, R=0.28, p=0.35). However, when considering only samples from which *D. longicaudata* was recovered, there was a significant negative relationship during Week 20 (Figure 4-18).

Temperature Measurements

Considering the apparent negative relationship between cold winter temperatures and presence of this species (Chapter 3), it was hypothesized that the abundance of *D. longicaudata* at Ft. DeNaud relative to LaBelle may be the result of warmer winter temperatures. It was furthermore hypothesized that the river may have a moderating effect on temperatures. Temperature variables obtained at five sites at LaBelle and Ft. DeNaud are detailed in Table 4-2. The three coldest locations in all months, in terms of extreme minimum temperature, were the two locations at Ft. DeNaud and the site at LaBelle closest to the river. In terms of mean minimum temperatures, both Ft. DeNaud sites were significantly colder than two of the three LaBelle sites (Table 4-3). Contrary to expectations, the LaBelle site farthest from the river was the warmest location in terms of

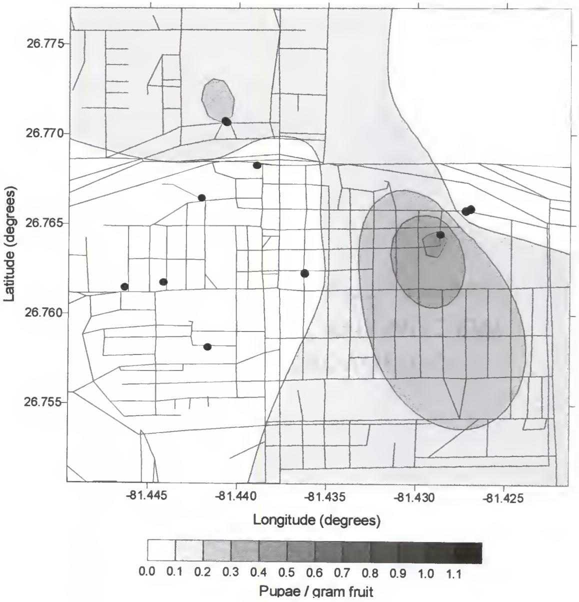

Figure 4-2. Spatial distribution of Caribbean fruit fly infestation of Surinam cherry fruits at LaBelle during the 14th week of 1996. Circles indicate locations of hosts sampled. Flies were recovered from 7 of 11 hosts.

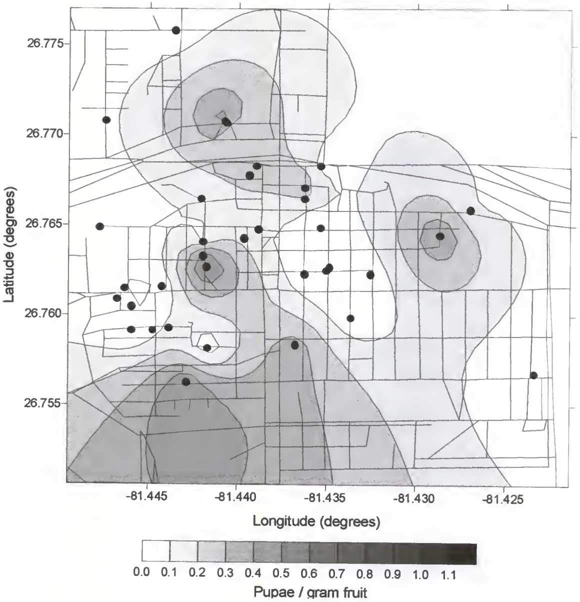

Figure 4-3. Spatial distribution of Caribbean fruit fly infestation of Surinam cherry fruits at LaBelle during the 16th week of 1996. Circles indicate locations of hosts sampled. Flies were recovered from 31 of 35 hosts.

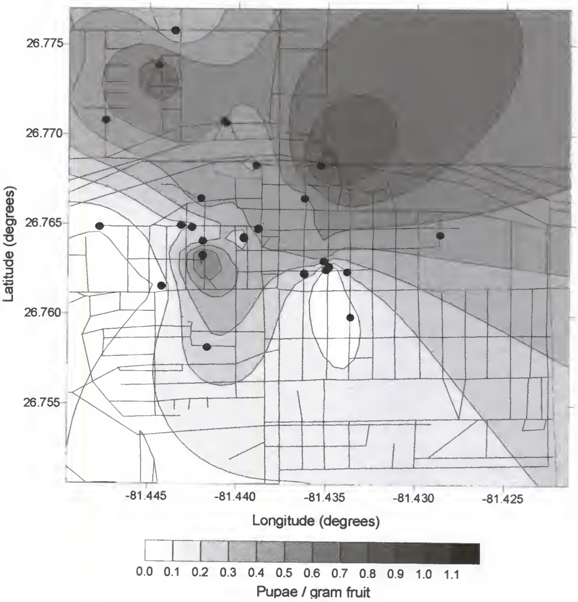

Figure 4-4. Spatial distribution of Caribbean fruit fly infestation of Surinam cherry fruits at LaBelle during the 18th week of 1996. Circles indicate locations of hosts sampled. Flies were recovered from 24 of 25 hosts.

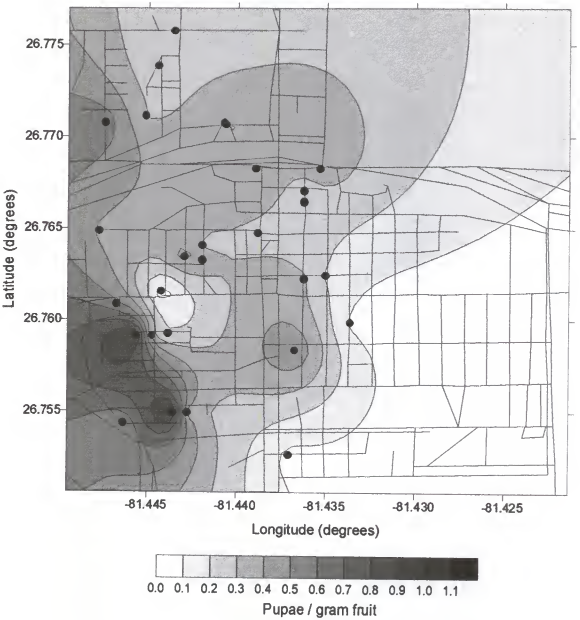

Figure 4-5. Spatial distribution of Caribbean fruit fly infestation of Surinam cherry fruits at LaBelle during the 20th week of 1996. Circles indicate locations of hosts sampled. Flies were recovered from 28 of 28 hosts.

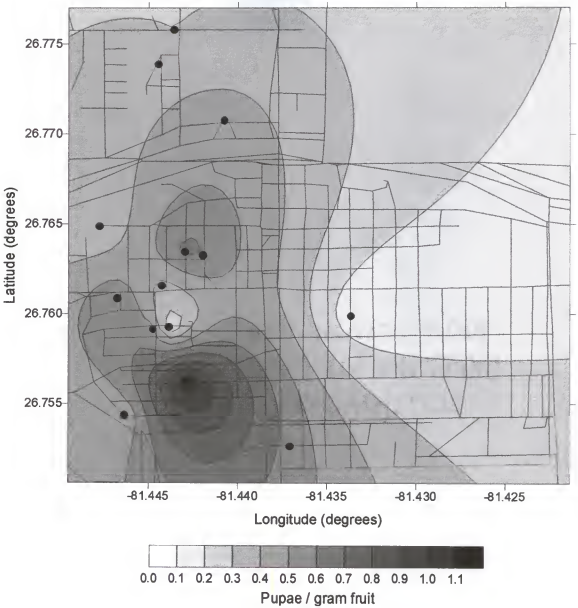

Figure 4-6. Spatial distribution of Caribbean fruit fly infestation of Surinam cherry fruits at LaBelle during the 22nd week of 1996. Circles indicate locations of hosts sampled. Flies were recovered from 14 of 14 hosts.

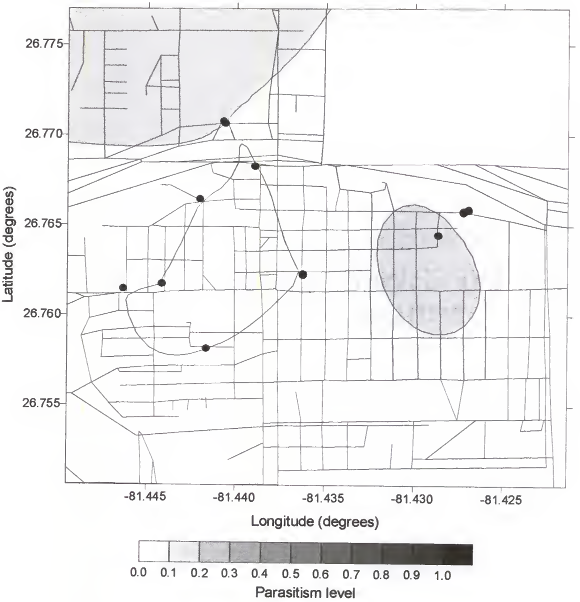

Figure 4-7. Spatial distribution of parasitism by *Doryctobracon areolatus* in Surinam cherry fruits at LaBelle during the 14th week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 2 of 11 hosts. Parasitism level is the ratio between the number of *D. areolatus* emerging and the number of all parasitoids and flies emerging.

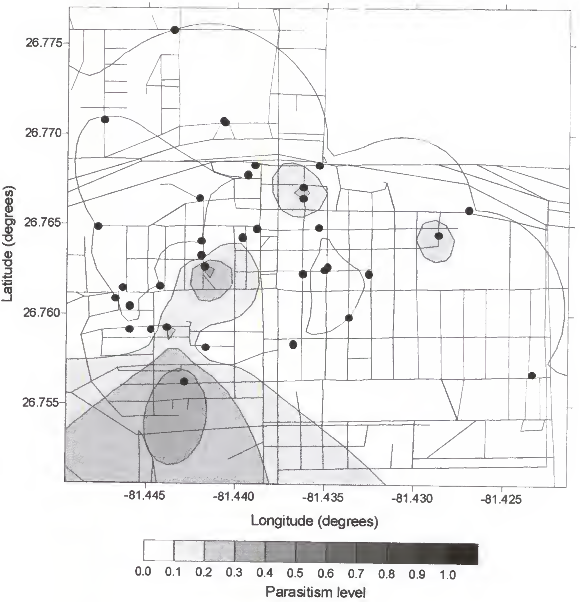

Figure 4-8. Spatial distribution of parasitism by *Doryctobracon areolatus* in Surinam cherry fruits at LaBelle during the 16th week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 11 of 35 hosts. Parasitism level is the ratio between the number of *D. areolatus* emerging and the number of all parasitoids and flies emerging.

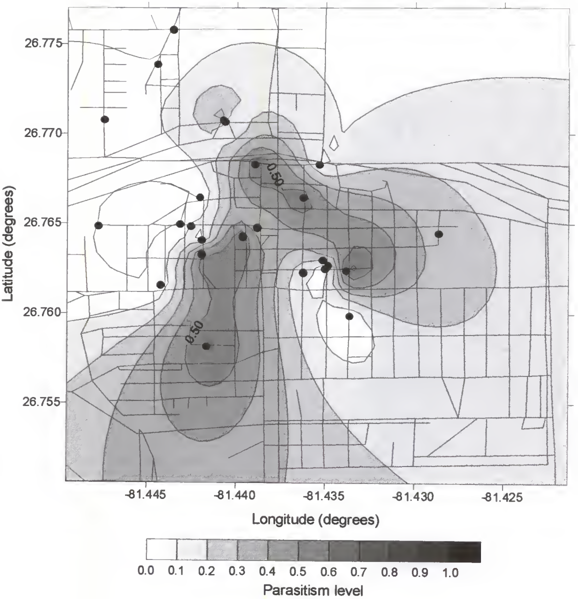

Figure 4-9. Spatial distribution of parasitism by *Doryctobracon areolatus* in Surinam cherry fruits at LaBelle during the 18th week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 15 of 25 hosts. Parasitism level is the ratio between the number of *D. areolatus* emerging and the number of all parasitoids and flies emerging.

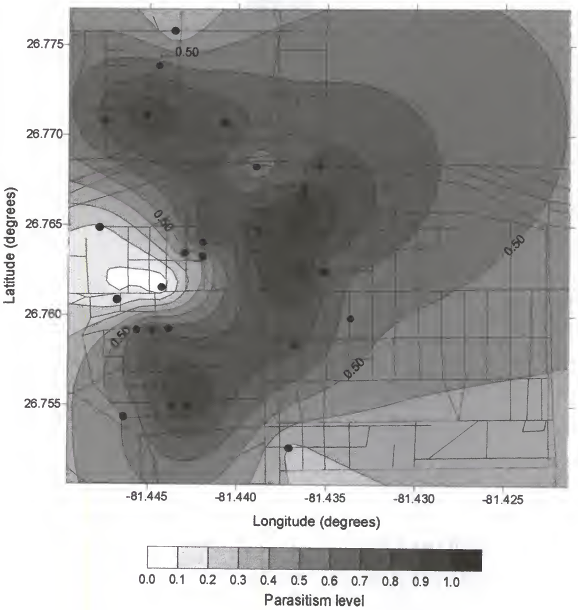

Figure 4-10. Spatial distribution of parasitism by *Doryctobracon areolatus* in Surinam cherry fruits at LaBelle during the 20th week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 27 of 28 hosts. Parasitism level is the ratio between the number of *D. areolatus* emerging and the number of all parasitoids and flies emerging.

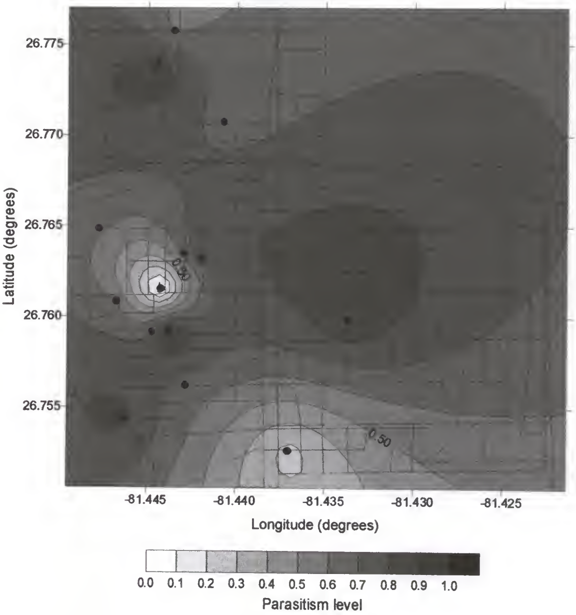

Figure 4-11. Spatial distribution of parasitism by *Doryctobracon areolatus* in Surinam cherry fruits at LaBelle during the 22nd week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 13 of 14 hosts. Parasitism level is the ratio between the number of *D. areolatus* emerging and the number of all parasitoids and flies emerging.

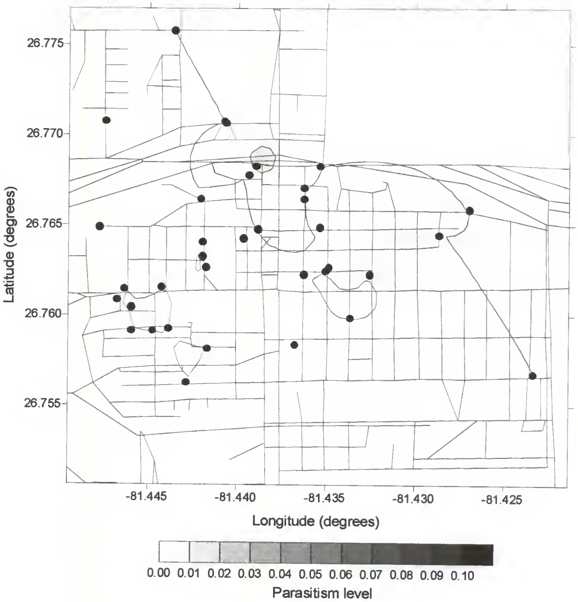

Figure 4-12. Spatial distribution of parasitism by *Diachasmimorpha longicaudata* in Surinam cherry fruits at LaBelle during the 16th week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 1 of 35 hosts. Parasitism level is the ratio between the number of *D. longicaudata* emerging and the number of all parasitoids and flies emerging.

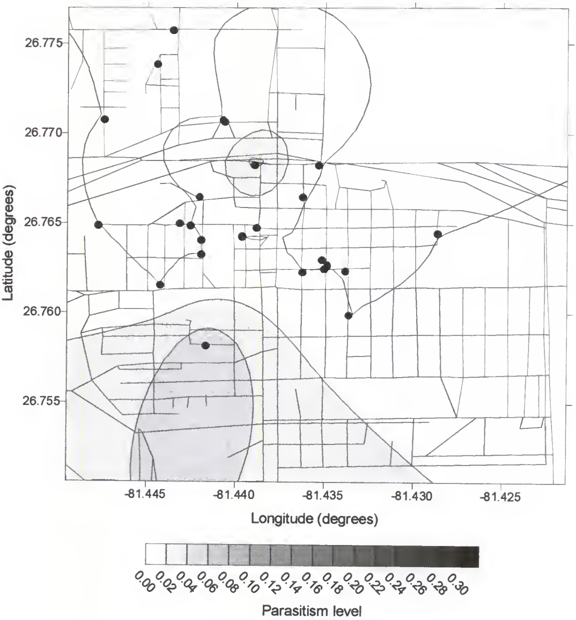

Figure 4-13. Spatial distribution of parasitism by *Diachasmimorpha longicaudata* in Surinam cherry fruits at LaBelle during the 18th week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 2 of 25 hosts. Parasitism level is the ratio between the number of *D. longicaudata* emerging and the number of all parasitoids and flies emerging.

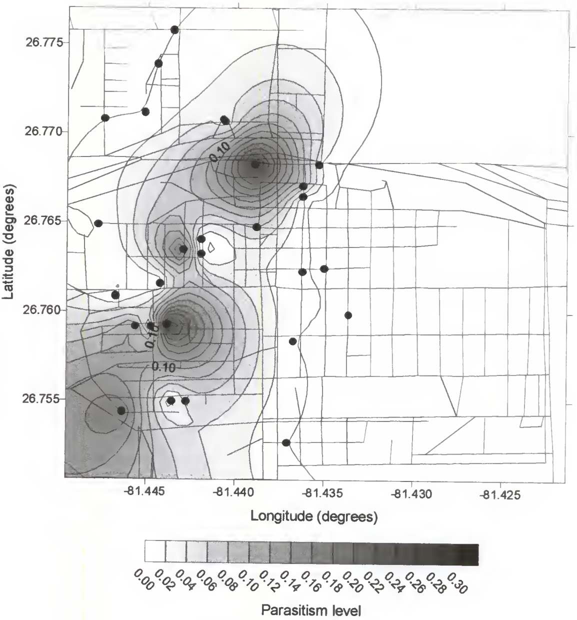

Figure 4-14. Spatial distribution of parasitism by *Diachasmimorpha longicaudata* in Surinam cherry fruits at LaBelle during the 20th week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 11 of 28 hosts. Parasitism level is the ratio between the number of *D. longicaudata* emerging and the number of all parasitoids and flies emerging.

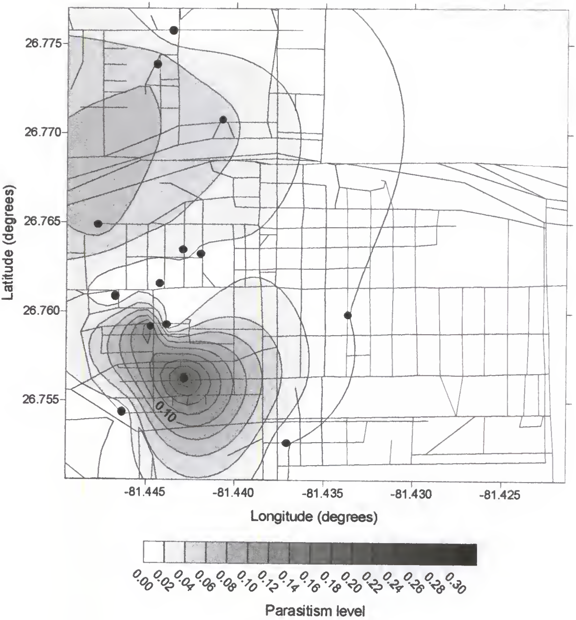

Figure 4-15. Spatial distribution of parasitism by *Diachasmimorpha longicaudata* in Surinam cherry fruits at LaBelle during the 22nd week of 1996. Circles indicate locations of hosts sampled. Parasitoids were recovered from 8 of 14 hosts. Parasitism level is the ratio between the number of *D. longicaudata* emerging and the number of all parasitoids and flies emerging.

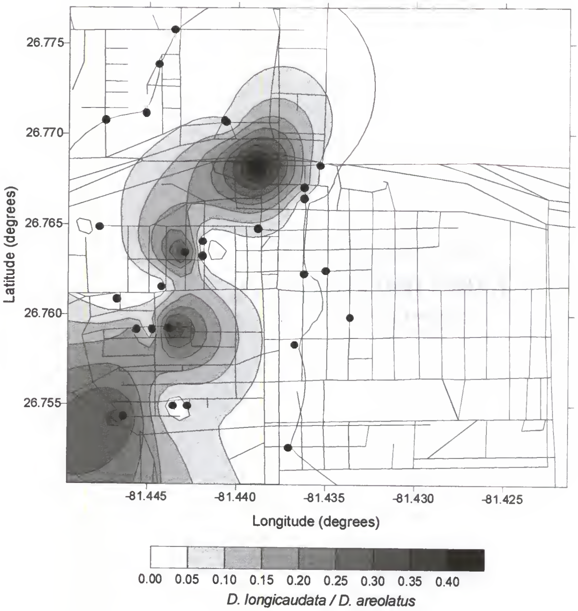

Figure 4-16. Contour map of the ratio between parasitism by *Diachasmimorpha longicaudata* and that by *Doryctobracon areolatus* in Surinam cherry fruits at LaBelle during the 20th week of 1996. Circles indicate locations of hosts sampled.

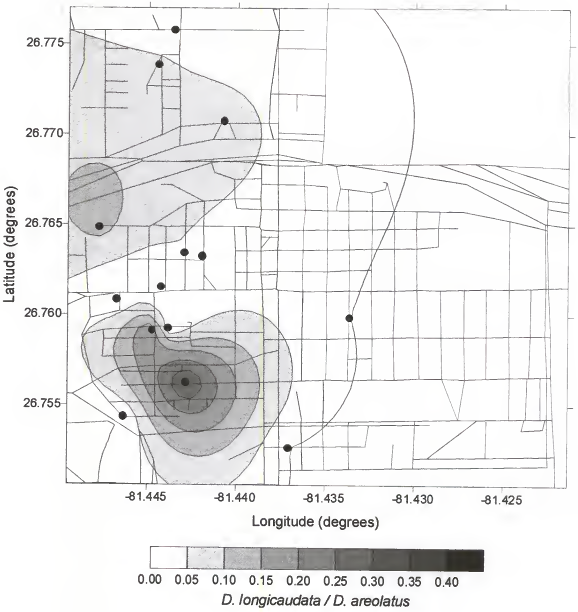

Figure 4-17. Contour map of the ratio between parasitism by *Diachasmimorpha longicaudata* and that by *Doryctobracon areolatus* in Surinam cherry fruits at LaBelle during the 22nd week of 1996. Circles indicate locations of hosts sampled.

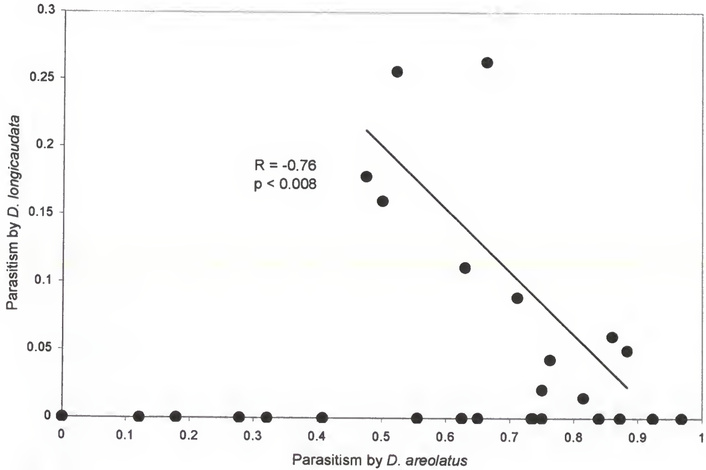

Figure 4-18. Relationship between parasitism by *Doryctobracon areolatus* and parasitism by *Diachasmimorpha longicaudata* in Surinam cherry fruits at LaBelle during week 20 of 1996. The correlation analysis was performed only on samples which produced *D. longicaudata*.

Table 4-2. Temperatures measured at various locations in LaBelle and Ft. DeNaud from December 1996 through March 1997.

Town	Distance and direction from river	Month	Temperature				
			Mean	Mean minimum	Extreme minimum	Mean maximum	Extreme maximum
LaBelle	100 meters North	December	17.29	11.19	2.74	24.60	28.56
		January	17.11	10.60	-3.38	24.74	29.31
		February	20.77	14.52	3.52	28.47	32.28
		March	22.95	16.31	13.06	30.27	33.42
	750 meters South	December	17.47	11.97	3.94	27.47	31.2
		January	17.67	11.42	-2.49	27.19	33.08
		February	21.38	14.96	4.33	32.24	39.02
		March	24.12	16.83	13.81	38.45	44.63
	1000 meters South	December	17.53	11.73	3.91	24.60	28.59
		January	17.20	11.17	-2.97	24.66	29.68
		February	20.61	14.98	3.91	27.91	32.29
		March	23.18	16.81	13.77	30.74	34.21
Ft. DeNaud	10 meters North	December	17.50	11.07	3.58	25.66	29.74
		January	17.25	10.44	-3.34	25.62	30.12
		February	20.78	14.39	2.42	29.04	32.72
		March	23.30	16.19	13.12	31.60	35.04
	210 meters South	December	17.63	11.15	3.12	25.18	30.03
		January	17.24	10.29	-4.29	25.34	31.15
		February	21.14	14.18	1.95	30.28	35.74
		March	23.66	15.70	11.62	33.86	38.14

Table 4-3. Mean ranks of temperatures among sites for various months from December 1996 through March 1997. Higher ranks indicate higher temperature readings.

Site[a]	Mean temperature[b]				Minimum temperature[b]				Maximum temperature[b]			
	December	January	February	March	December	January	February	March	December	January	February	March
1	2.90 BC	2.84 B	1.46 D	2.13 D	3.56 B	3.79 B	3.64 B	2.88 B	2.06 D	1.87 D	1.21 E	2.00 D
2	1.38 D	1.97 C	2.43 C	1.42 E	2.24 C	2.27 C	2.50 C	2.66 C	1.50 E	1.81 D	2.00 D	1.16 E
3	4.77 A	4.74 A	4.75 A	4.84 A	4.68 A	4.77 A	4.21 A	4.35 A	4.87 A	4.87 A	4.79 A	4.87 A
4	3.23 B	2.68 B	3.93 B	3.81 B	2.19 C	1.83 D	1.93 D	1.61 D	2.69 C	2.90 C	3.89 B	4.10 B
5	2.71 C	2.77 B	2.43 C	2.81 C	2.32 C	2.32 C	2.71 C	2.48 C	3.87 B	3.55 B	3.11 C	2.87 C

[a] Site 1 = LaBelle, 100 meters north of the Caloosahatchee River.
Site 2 = LaBelle, 750 meters south of the Caloosahatchee River.
Site 3 = LaBelle, 1000 meters south of the Caloosahatchee River.
Site 4 = Ft. DeNaud, 10 meters north of the Caloosahatchee River.
Site 5 = Ft. DeNaud, 210 meters south of the Caloosahatchee River.

[b] Means within a column followed by the same letter are not significantly different, $p=0.05$, according to the Waller-Duncan k-ratio t test, and k-ratio=100.

mean, mean minimum and mean maximum temperatures for all months. Interestingly, the two Ft. DeNaud sites were warmer than the other two LaBelle locations for all months in terms of mean maximum temperature. With the exception of a possible positive effect of high maximum temperature on *D. longicaudata*, these measurements failed to explain the differences in parasitoid abundance between the two towns. Note, however, that these measurements were performed the winter following fruit sampling in this study. Thus, it is possible that they are not representative of the true situation during the previous year.

For the LaBelle sites, there is a possible relationship between minimum temperatures and parasitism by *D. longicaudata*. At the warmest site (81.444 West, 26.759 North, 1000 meters south of river) parasitism by *D. longicaudata* was highest (26.3% during Week 20). At the coldest site (81.436 West, 26.762 North, 750 meters south of river) *D. longicaudata* was not recovered. The third site (81.441 West, 26.771 North, 100 meters north of river) was intermediate in terms of both temperature and parasitism (4.7% during week 22). Thus, a local effect of low winter temperatures cannot be dismissed. However, temperatures need to be measured at a larger number of sites in order to substantiate such a relationship.

Comparisons Among Years

The pattern of parasitism by *D. areolatus* was somewhat similar for all years (Figure 4-19). Mean parasitism reached a peak of 30-60% in May or June, corresponding to the peak of Surinam cherry availability. This was expected, as parasitism rates are usually higher in Surinam cherry than in loquat or guava (see Table 3-6). Mean parasitism was higher in loquat (early spring) during 1991-1993 than during 1994-1996. In all three years there was significantly higher parasitism than in 1996. However, only in

1993 was it significantly higher than in 1994 or 1995 (Figure 4-21). There was an apparent gradual decrease in parasitism in Surinam cherry from 1991 through 1994, followed by an increase in 1995 and decrease again in 1996. However, these differences among years were not significant (Figure 4-22).

Temporal patterns of parasitism by *D. longicaudata* were much more variable (Figure 4-20). Peak abundance in spring for various years ranged from 4% in 1996 to 23% in 1994, and was observed in either April, May or June. Note the very similar patterns in 1991 and 1996. In both years, parasitism in early spring was at or close to zero, with mean parasitism reaching a peak of less than 5% in June. The unusually high peak in August 1991 should be treated with caution, as it is a mean of only four samples. Parasitism in loquat was significantly higher during 1995 than during either 1991, 1994 or 1996 (Figure 4-21). Parasitism in loquat during 1992 and 1993 was not significantly different than in any other year. In Surinam cherry, parasitism during 1993, 1994, and 1995 was significantly higher than during other years, while parasitism in 1995 was higher than in all other years except for 1994 (Figure 4-22).

Mean parasitism by *D. areolatus* in loquat was higher than that by *D. longicaudata* for all years except 1995 (Figure 4-21), but the difference was significant only during 1991 (paired-comparisons t test, $t=2.86$, $p<0.02$), 1993 ($t=5.23$, $p<0.0001$), and 1996 ($t=3.55$, $p<0.0009$), and not 1992 ($t=1.58$, $p=0.13$), 1994 ($t=2.24$, $p=0.09$), or 1995 ($t=1.37$, $p=0.18$). Parasitism by *D. areolatus* in Surinam cherry was significantly higher than that by *D. longicaudata* for all years (1991, $t=7.95$, $p<0.0001$; 1992, $t=8.59$, $p<0.0001$; 1993, $t=3.83$, $p<0.0005$; 1994, $t=4.68$, $p<0.0003$; 1995, $t=2.97$, $p<0.007$; 1996, $t=10.86$, $p<0.0001$).

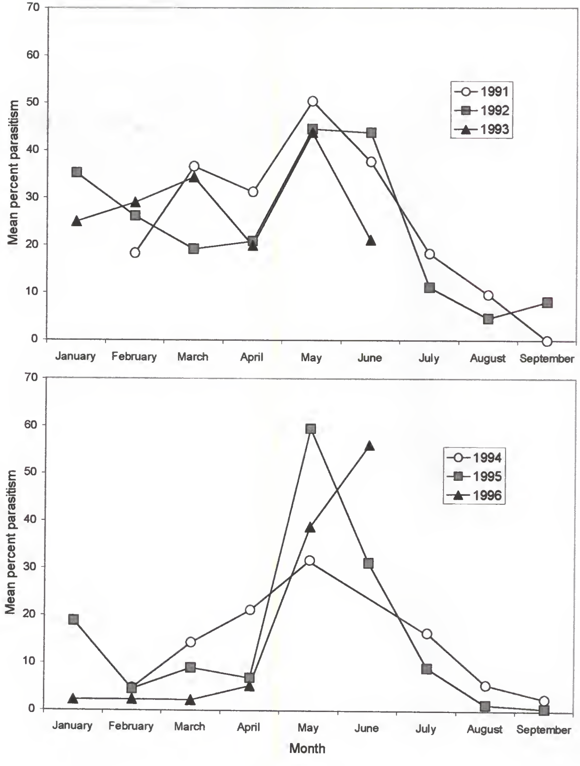

Figure 4-19. Parasitism by *Doryctobracon areolatus* at LaBelle during the years 1991-1996

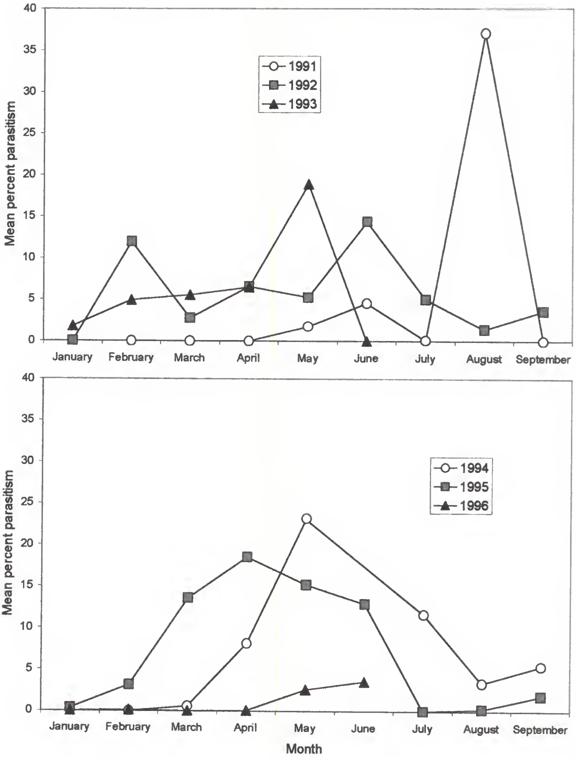

Figure 4-20. Parasitism by *Diachasmimorpha longicaudata* at LaBelle during the years 1991-1996.

Mean parasitism by *D. longicaudata* in loquat was significantly related with extreme minimum temperature of the previous December (Figure 4-23). Note that during the three years following a cold December, parasitism was at or close to zero.

Mean parasitism by *D. areolatus* in loquat was significantly related with several environmental variables. The most significant was extreme minimum temperature of the previous January (Figure 4-24). Other significant variables included mean minimum January temperature (R^2=0.68, F=8.60, $p<0.05$), mean January temperature (R^2=0.75, f=11.73, $p<0.03$), and October precipitation (negative relationship, R^2=0.86, F=25.17, $p<0.008$).

There were highly significant relationships between parasitism by *D. longicaudata* in Surinam cherry and both mean and mean minimum December temperatures (Figures 4-25 and 4-26). Other variables significantly related with *D. longicaudata* abundance in Surinam cherry included mean November temperatures (R^2=0.66, F=7.91, $p<0.05$), mean March temperature (R^2=0.86, F=24.16, $p<0.008$), mean maximum November temperatures (R^2=0.67, F=8.44, $p<0.05$), and December precipitation (R^2=0.80, F=15.52, $p<0.02$).

Mean parasitism by *D. areolatus* in Surinam cherry was significantly related with mean February temperatures (R^2=0.76, F=12.77, $p<0.03$). The lack of highly significant relationships was not surprising, given the relatively high parasitism levels during all years, and the lack of significant differences among years.

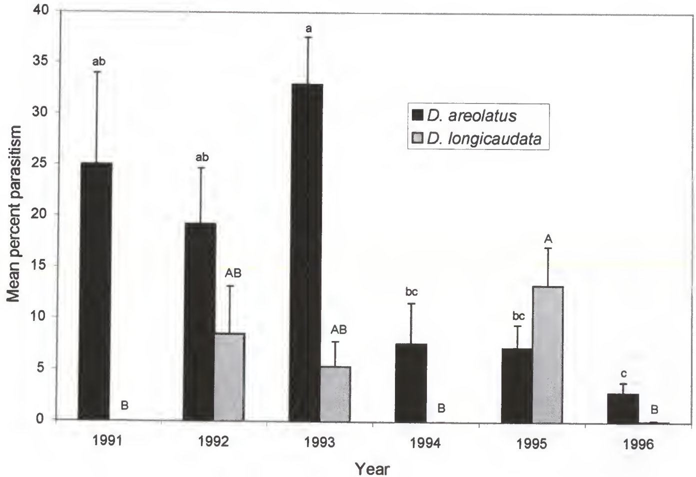

Figure 4-21. Mean parasitism levels by *Doryctobracon areolatus* and *Diachasmimorpha longicaudata* in loquat fruits at LaBelle during the years 1991-1996. Bars with the same lower-case letter (*D. areolatus*) and bars with the same upper-case letter (*D. longicaudata*) are not significantly different, according to the Waller-Duncan k-ratio t test, and k-ratio=100.

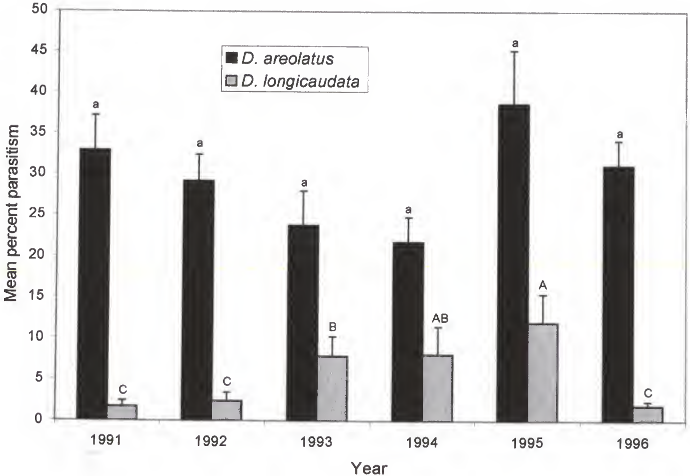

Figure 4-22. Mean parasitism levels by *Doryctobracon areolatus* and *Diachasmimorpha longicaudata* in Surinam cherry fruits at LaBelle during the years 1991-1996. Bars with the same lower-case letter (*D. areolatus*) and bars with the same upper-case letter (*D. longicaudata*) are not significantly different, according to the Waller-Duncan k-ratio t test, and k-ratio=100.

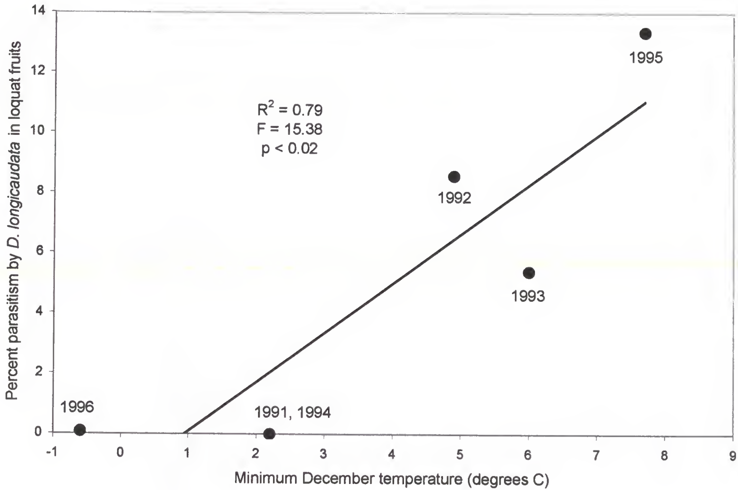

Figure 4-23. Relationship between minimum temperature during the month of December and parasitism by *Diachasmimorpha longicaudata* in loquat fruits the following spring.

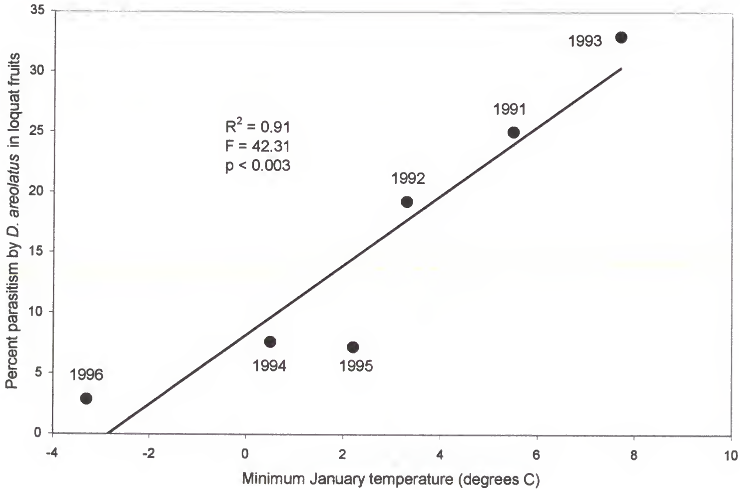

Figure 4-24. Relationship between minimum temperature during the month of January and parasitism by *Doryctobracon areolatus* in loquat fruits the following spring.

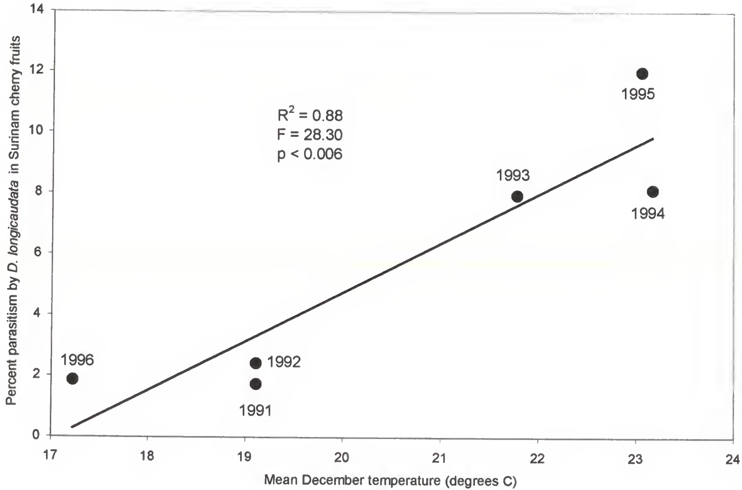

Figure 4-25. Relationship between mean temperature during the month of December and parasitism by *Diachasmimorpha longicaudata* in Surinam cherry fruits the following spring.

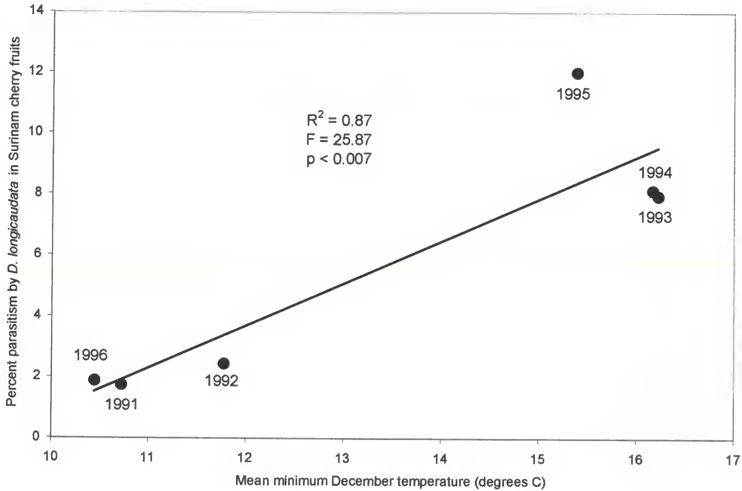

Figure 4-26. Relationship between mean minimum temperature during the month of December and parasitism by *Diachasmimorpha longicaudata* in Surinam cherry fruits the following spring.

Discussion

Results of the large-scale geographical study (Chapter 3) suggest that cold winter temperatures may have a negative effect on *D. longicaudata* populations. Analyses of the variability in parasitism among years suggest that cold temperatures have some effect on both *D. longicaudata* and *D. areolatus*. While minimum January temperatures appear to influence parasitism by *D. areolatus* in loquat, populations of this species appear to rebound to the point that no significant differences are observed among years in parasitism in Surinam cherry. The effects of cold winter temperatures appear to have a more profound affect on *D. longicaudata*. In years with cold minimum December temperatures, parasitism by this species in loquat is at or near zero. In the coldest years, populations fail to recover fully, with mean parasitism in Surinam cherry staying below 5%.

The apparent relationships between January temperatures and *D. areolatus* abundance on one hand, and between December temperatures and *D. longicaudata* abundance on the other, suggest that the two species may be influenced by different environmental factors, whether direct temperature affects or indirect influence of temperature through host availability. This study does not fully resolve which of these factors may be important.

Only during 1995 was *D. longicaudata* more abundant (though not significantly) than *D. areolatus* in loquat. The 1994 fall season was unique among the years of this study in that an unusual crop of loquat occurred during this time (Tim Holler, pers. comm.). Thus, there was a supply of hosts bridging the usual gap between common guava in late summer and loquat in early spring, making the temporal availability of hosts

more similar to that normally observed on the southeastern coast of Florida. These observations support the hypothesis suggested in Chapter 3 that *D. longicaudata* benefits from a relatively constant supply of hosts.

An examination of distribution among Surinam cherry trees during 1996 may shed light on parasitoid population dynamics, at least for years following cold winters. *D. areolatus* was initially recovered only from hosts with highest *A. suspensa* densities. In subsequent weeks, however, there was no relationship between fly densities and parasitoid abundance. Given the increase in fly densities over time, this suggests that parasitoids are dependent on fly abundance only when densities are low.

D. longicaudata was not recovered during the first collection week, and was found in a large number of trees only six weeks later, or four weeks after *D. areolatus* was widely distributed. These differential temporal dynamics of the two parasitoid species are similar to those reported by Sivinski et al. (1998) within individual trees. Both species appear to initially occur at several focal points, from which they disperse to other host trees. However, while *D. areolatus* is abundant in most trees at the peak of the fruiting period, *D. longicaudata* populations at this time are still concentrated around the focal points due to its late colonization.

The significance of focal points in the dynamics of parasitoid populations, as well as effects of local temperatures at specific hosts, would depend on the degree of dispersal. Little is known about dispersal of fruit fly parasitoids. Messing et al. (1994, 1995) studied the short-range (10-40 m) dispersal of mass-reared parasitoids of three species, including *D. longicaudata*. Further studies on medium- and long-range dispersal in field populations is necessary. Note that abundance of the various parasitoid species differs

greatly between LaBelle and Ft. DeNaud. This suggests that long-range (>1 km) dispersal may be limited.

The relationship between *D. areolatus* and *D. longicaudata* appears to be quite complex. A positive relationship was observed during Week 18, i.e., the second week during which *D. longicaudata* was recovered. The two host trees from which *D. longicaudata* was collected also were among the highest in terms of parasitism by *D. areolatus*. This suggests that environmental factor(s) may be similarly influencing both presence of *D. longicaudata* and abundance of *D. areolatus* during this week. However, such a relationship was not observed in subsequent weeks. During the peak of fruit availability (Week 20) parasitism levels of *D. areolatus* in samples containing *D. longicaudata* did not differ significantly from parasitism in samples from which *D. longicaudata* was absent ($t=1.04$, $p=0.31$). Thus, presence of *D. longicaudata* in a particular tree appears to be unrelated with the abundance of *D. areolatus*. However, once *D. longicaudata* arrives at a host, it has an apparent negative effect on *D. areolatus* abundance. Hence the negative relationship between the two parasitoids when only trees with *D. longicaudata* present are considered (Figure 4-18). Lack of niche separation within tree canopies (Sivinski et al., in preparation) suggests a potential for competitive interactions.

For a specific example, consider the Surinam cherry tree at coordinates 26.768 North, 81.439 West. During Week 18, it had one of the highest levels of parasitism by *D. areolatus*, at 61% (Figure 4-9). This was also one of the two hosts from which *D. longicaudata* was recovered that week (Figure 4-13). Parasitism by *D. areolatus* in this tree declined to 52% by Week 20, while increasing to over 70% in all adjacent hosts

(Figure 4-10). At the same time, parasitism by *D. longicaudata* increased to 26%, while remaining uncommon in surrounding trees (Figure 4-14).

Alternating warm and cold winters may contribute to the coexistence of the two parasitoid species at LaBelle. Warm winters, which may positively contribute to host availability, allow increases in *D. longicaudata* populations. If the frequency of warm winters was to increase, it would enable consistently high population levels, thus increasing the competitive pressure on *D. areolatus*. Under certain circumstances this could lead to the displacement of *D. areolatus*, as discussed in Chapter 3. Conversely, cold winters like that of 1995-1996 cause a severe reduction in populations of this species. If the frequency of cold winters was to increase, *D. longicaudata* populations may be suppressed to a level from which they could not recover, leading to extinction. These scenarios may explain the absence of *D. areolatus* in southeastern Florida, where winters are warmer than at LaBelle, and the absence of *D. longicaudata* in central Florida, where winters are colder, while they coexist in the intermediate climate of LaBelle.

CHAPTER 5
EFFECTS OF TEMPERATURE ON IMMATURE DEVELOPMENT, ADULT LONGEVITY AND OVIPOSITIONAL ACTIVITY IN *DIACHASMIMORPHA LONGICAUDATA*

The temporal and spatial distribution patterns of *Diachasmimorpha longicaudata* (Ashmead) in Florida suggest that low temperatures may have a negative effect on this species (Chapters 3 and 4). One hypothesis proposed is that temperatures affect the parasitoids directly, causing increased mortality. The objective of this chapter is to determine the temperature tolerances of immature and adult *D. longicaudata*. Additionally, temperature effects on arrested immature development and adult ovipositional activity are examined.

Materials and Methods

Immature Development

D. longicaudata used in this experiment were tenth generation of a stock descending from individuals collected at LaBelle, Florida. Fifty female parasitoids were placed in each of twelve 20 cm^2 screen cages. An oviposition unit (see description in Chapter 6) containing several hundred late third-instar Caribbean fruit fly, *Anastrepha suspensa* (Loew), larvae was placed on top of each cage for ca. 3 hr. Upon completion of this exposure period, the larvae were placed upon moist fine vermiculite (15-20 ml water per 100 cm^3 vermiculite) in small plastic containers. Containers were covered with lids with fine-mesh posh fabric. Larvae were allowed to enter the vermiculite for pupation at

25°C for several hours. Containers were subsequently transferred to Florida Reach-In® environmental chambers (Gaffney Engineering, Inc., Gainesville, Florida, see Walker et al. 1993). Containers were randomly placed in each of six chambers, set at constant temperatures of 11, 13, 15, 17, 19 or 21°C (±0.2°C) and 90% relative humidity. Additionally, a container with unexposed host larvae was placed in each chamber as a control. This procedure was repeated for a total of six days. On the first two days, oviposition units contained ca. 700 host larvae. Following a break of four days, parasitoids were exposed to hosts for an additional four consecutive days, with oviposition units containing ca. 300-400 host larvae. Two containers with larvae exposed to parasitoids were placed in each chamber on each of the six days, for a total of 12 samples, except 21°C where only 8 samples were placed in the chamber over the final four day period.

Parasitoid emergence was recorded daily until ca. 19 weeks after the median exposure date, and then weekly until termination of the experiment. Containers were removed from most chambers and placed in a room at 25°C ca. 21 weeks after exposure. Those samples at 15 or 17°C remained for an additional 4 weeks. Weekly emergence counts continued until 29 weeks after exposure, when no more emergence was observed. Note that temperature control failed 13 weeks after exposure in the chamber set at 19°C. As a result the temperature dropped to approximately 12°C, and remained at this level until removal of the samples 8 weeks later.

Following termination of the experiment, the vermiculite was sifted and the number of host puparia, with and without fungi, was counted. Parasitoid emergence was

estimated as the ratio between the number of parasitoids emerging and the number of puparia without fungi.

Adult Longevity and Ovipositional Activity

Insects were obtained from the mass-rearing facility, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, Florida. Parasitoids had been in colony for ca. 30 generations.

Twenty newly emerged *D. longicaudata*, 10 females and 10 males, were placed in 20 cm^3 screen cages, and provided within honey-agar and water. Eight of these cages were placed upon two shelves within each of six Florida Reach-In environmental chambers. The chambers were set at constant temperatures of 15, 19, 23, 27, 31, or 35°C (±0.2°C). All chambers were set at the same saturation deficit, corresponding to relative humidities of 44, 57, 66, 73, 79, and 83%, respectively. Parasitoids were presented with 100 irradiated late third instar *A. suspensa* larvae for 70 min twice a week. Exposure was during the third hour of a 12 hr photophase, which preliminary experiments indicated was a period of relatively high ovipositional activity at room temperature.

Mortality was recorded daily until the death of the last parasitoid. Ovipositional activity was estimated by counting the progeny resulting from the first two host exposures, at ages of 4 and 7 days. Progeny production is known to be highest during the first week of adult life (Greany et al. 1976).

Results

Immature Development

D. longicaudata emergence increased with temperature (Figure 5-1). No parasitoids emerged at 11°C, and at 13°C emergence averaged only 22%. No *A. suspensa* emerged in the control containers (pupae not exposed to parasitoids) at 11°C, and emergence in the controls at 13°C was only 52% of the mean emergence at higher temperatures. For comparison, *D. longicaudata* emergence at 13°C was 31, 28, 27 and 26% of that at 15, 17, 19 and 21°C, respectively. Thus, host mortality may be partially, though apparently not totally, responsible for the low parasitoid emergence at low temperatures.

Sex ratio (percent males) of the emerging parasitoids increased with temperature (Figure 5-2). Only 3% of the individuals emerging at 13°C were males. Thus, males suffered a higher degree of mortality than females at low temperatures.

Temporal distributions of *D. longicaudata* emergence at various temperatures are illustrated in Figures 5-3 through 5-7. Emergence commenced on days 20, 25, 32 and 49, and peaked on days 24, 30, 39 and 57, for 21, 19, 17 and 15°C, respectively. At 13°C, only 13 individuals emerged between days 78 and 101.

The proportion of individuals emerging after the initial peak decreased with temperature (Figure 5-8). At 13°C, 97% of the parasitoids emerged following the transfer of containers from 13 to 25°C (Figure 5-3). At 15°C, mean daily emergence began to increase after ca. 140-150 days, and increased dramatically following transfer to 25°C

(Figure 5-4). Small numbers of parasitoids emerged almost continuously at 17°C (Figure 5-5), while at 21°C most of the late emergence occurred from day 113 (Figure 5-7).

Adult Longevity and Ovipositional Activity

Adult longevity was inversely related with temperature, averaging 58, 35, 30, 26, 18 and 5 days for females, and 49, 35, 22, 16, 10 and 3 days for males, at 15, 19, 23, 27, 31 and 35°C, respectively (Figure 5-9). Females lived significantly longer than males at 23°C ($t=4.20$ $p<0.0001$), 27°C ($t=4.88$, $p<0.0001$), 31°C ($t=6.49$, $p<0.0001$), and 35°C ($t=7.50$, $p<0.0001$), but not 15°C ($t=1.97$, $p=0.051$) or 19°C ($t=0.03$, $p=0.98$).

A preliminary experiment suggests that mortality does not increase at 13°C, but may increase at 11°C. Four cages with 10 females and 10 males were placed in each of two chambers set at these temperatures for 23 days. Mean mortality for this period was 12.5 and 32.5% for females and males, respectively, at 11°C, and 5 and 17% for females and males, respectively, at 13°C, compared to 10% for females and 12% for males at 15°C in the preceding experiment.

Ovipositional activity as estimated by progeny production on days 4 and 7 was significantly higher in cages placed on the lower shelf at most temperatures (19°C, $t=4.38$, $p<0.0006$; 23°C, $p=5.70$, $p<0.0001$; 27°C, $t=2.68$, $p<0.02$; 31°C, $t=4.77$, $p<0.0003$). The relatively low activity in the upper cages may be the result of air movement at the top of the chamber (note that the oviposition unit was placed on top of the cage). Therefore, in comparisons of ovipositional activity among temperatures only data from the cages on the lower shelf were used.

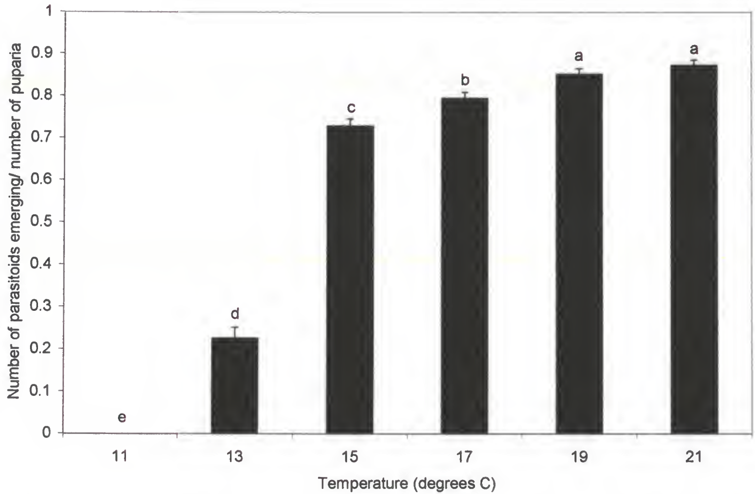

Figure 5-1. Emergence of *Diachasmimorpha longicaudata* at various constant temperatures. Includes data from the last four exposure dates (total of 8 samples per treatment). Data were subjected to an arcsine square-root transformation prior to analysis. Bars with the same letter are not significantly different, according to the Waller-Duncan k-ratio t test, and k-ratio=100.

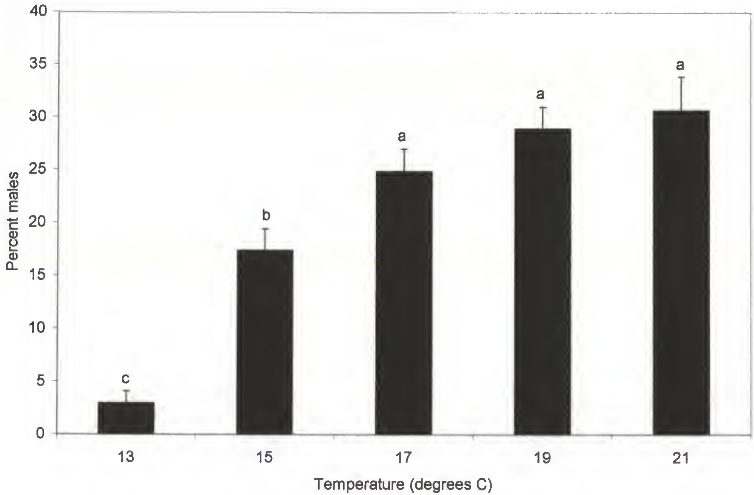

Figure 5-2. Sex ratio of *Diachasmimorpha longicaudata* emerging at various constant temperatures. Data were subjected to an arcsine square-root transformation prior to analysis. Bars with the same letter are not significantly different, according to the Waller-Duncan k-ratio t test, and k-ratio=100.

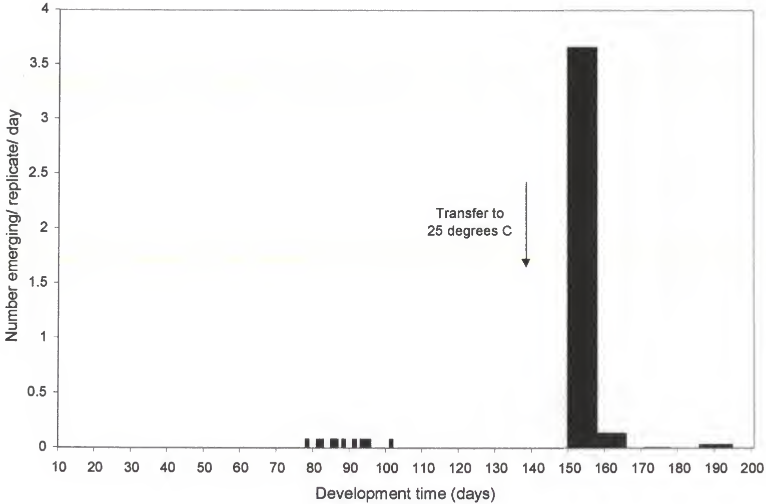

Figure 5-3. Temporal distribution of *Diachasmimorpha longicaudata* emergence at a constant temperature of 13°C.

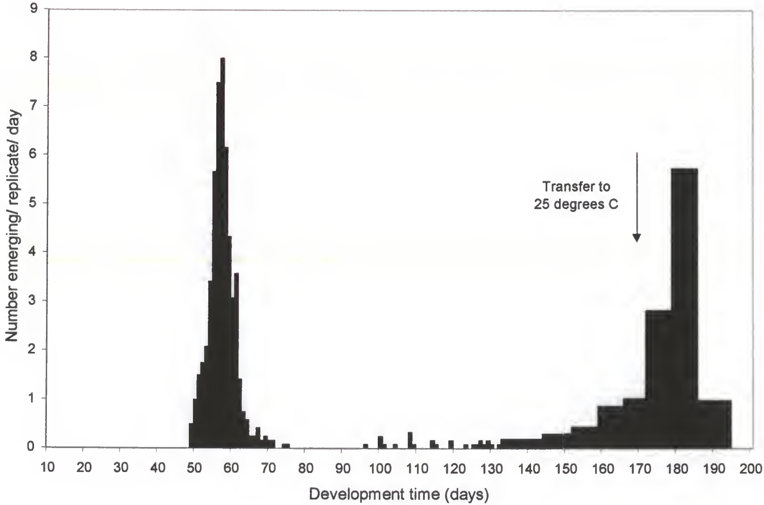

Figure 5-4. Temporal distribution of *Diachasmimorpha longicaudata* emergence at a constant temperature of 15°C.

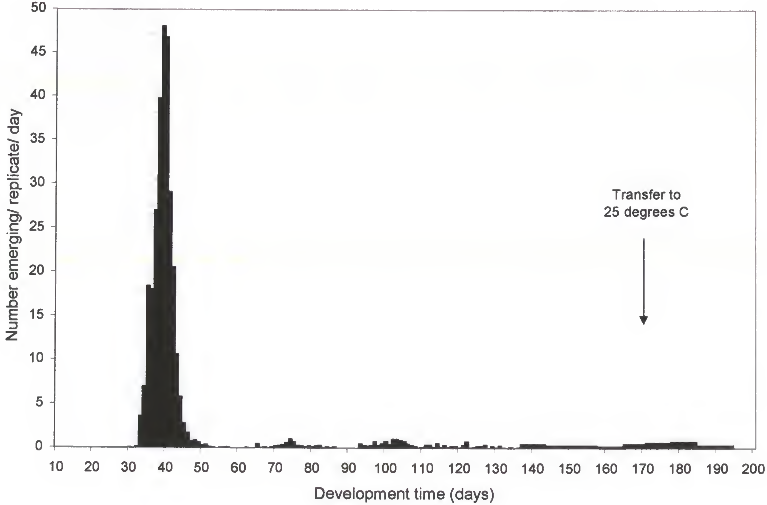

Figure 5-5. Temporal distribution of *Diachasmimorpha longicaudata* emergence at a constant temperature of 17°C.

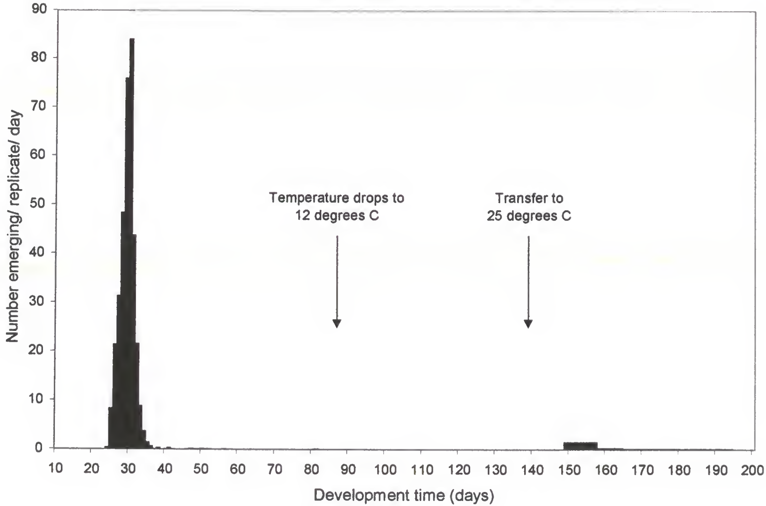

Figure 5-6. Temporal distribution of *Diachasmimorpha longicaudata* emergence at a constant temperature of 19°C.

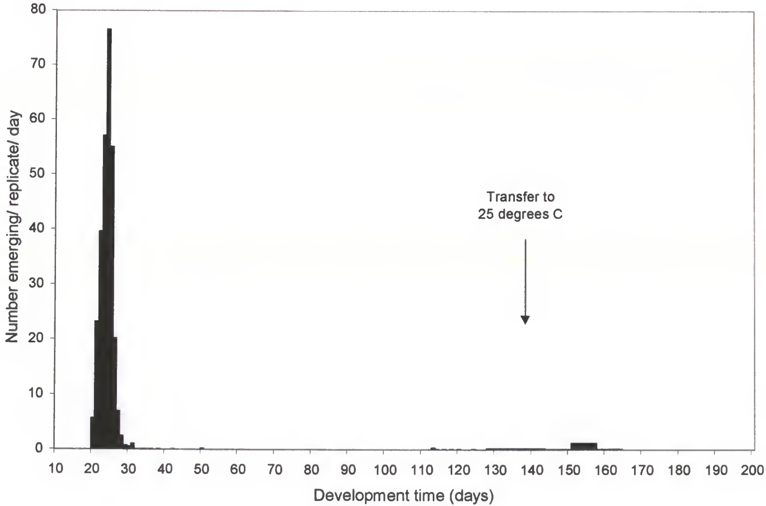

Figure 5-7. Temporal distribution of *Diachasmimorpha longicaudata* emergence at a constant temperature of 21°C.

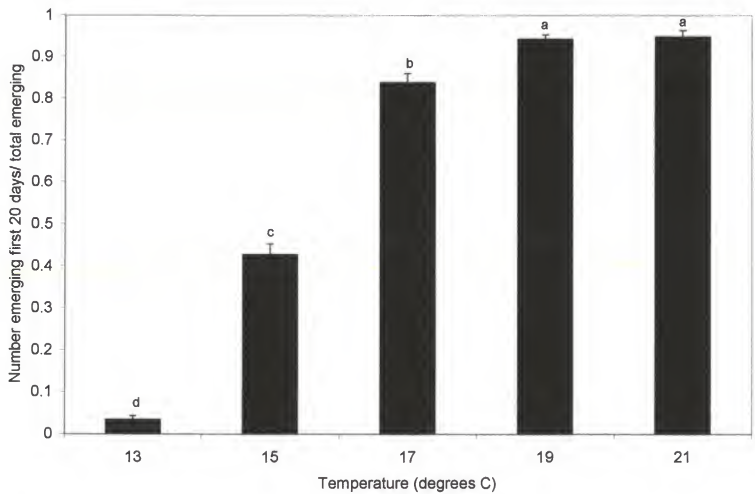

Figure 5-8. Ratio between the number of *Diachasmimorpha longicaudata* emerging within 20 days of the first emergence and the total number emerging at various constant temperatures. Data were subjected to an arcsine square-root transformation prior to analysis. Bars with the same letter are not significantly different, according to the Waller-Duncan k-ratio t test, and k-ratio=100.

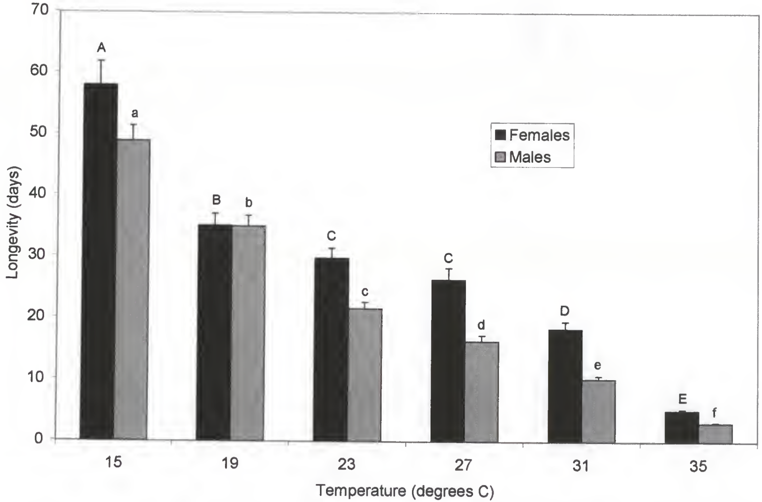

Figure 5-9. Longevity of *Diachasmimorpha longicaudata* females and males at various constant temperatures. Bars with the same upper-case (females) or lower-case (males) letter are not significantly different, according to the Waller-Duncan k-ratio t test, and k-ratio=100.

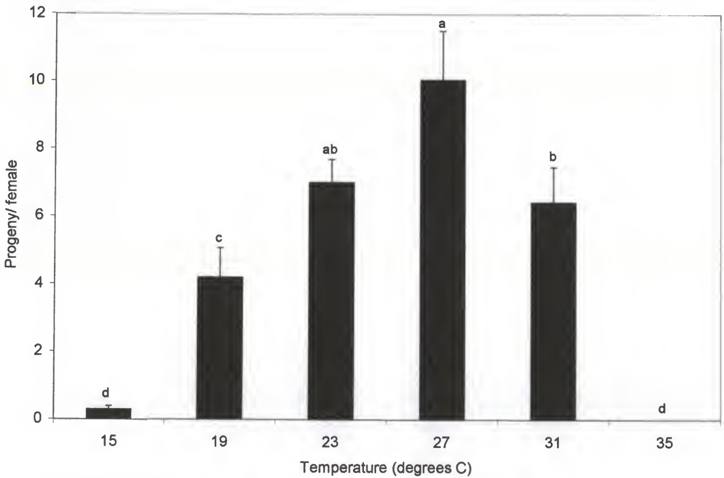

Figure 5-10. Numbers of progeny produced by *Diachasmimorpha longicaudata* females at various constant temperatures. Includes data from two exposures, at ages 4 and 7 days, in four cages on the bottom shelf of the environmental chambers, for a total of eight replicates per temperature treatment. Data were subjected to an arcsine square-root transformation prior to analysis. Bars with the same letter are not significantly different, according to the Waller-Duncan k-ratio t test, and k-ratio=100.

Progeny production was greatest at 27°C (though not significantly higher than at 23°), decreasing with lower and higher temperatures (Figure 5-10). No oviposition was apparent at 35°C.

Discussion

The late emergence of parasitoids suggests that some individuals undergo arrested development. This may be true diapause (involving induction and release by environmental factors) or non-diapause quiescence (see reviews by Tauber at al. (1983, 1986) for further explanation of these terms). Which of these processes may be occurring in *D. longicaudata* could not be determined.

The phenomenon of arrested development appears to increase at lower temperatures. Ashley et al. (1976), examining effects of high temperatures, observed an increase in delayed development of *D. longicaudata* larvae at the lowest temperature in their study (22°C). In the present study, delayed emergence was a common occurrence at 15°C, with over 50% of the individuals emerging after the initial peak. At 13°C, almost all parasitoids emerged only following transfer to room temperature. Thus it appears that a polymorphism occurs within the population, where some individuals delay their immature development for various lengths of time. This polymorphism is, however, related to temperature, peaking at 15°C.

D. longicaudata emergence decreases with temperature, is very low at 13°C, and no emergence was observed at 11°C. However, some of the mortality may be attributed to host mortality. No *A. suspensa* emerged at 11°C, which is similar to the 10°C development threshold determined by Prescott and Baranowski (1971). The low fly

emergence at 13°C could account for much, but not all, of the reduced parasitoid emergence at this temperature.

Studies with other fruit fly parasitoids have demonstrated somewhat less cold tolerance for the parasitoids than for their hosts. Loni (1997) calculated a slightly higher low temperature threshold for *Psyttalia concolor* (Szepligeti) than for its host *Bactrocera oleae* (Gmelin). *Psyttalia concolor* is apparently somewhat less cold tolerant than *D. longicaudata*; no parasitoids emerged at 13°C, and emergence at 15°C was less than 1%. However, it is unclear whether nonemerging individuals remained viable at low temperatures. *Doryctobracon crawfordi* (Viereck) is less tolerant to both low and high temperatures than its host *Anastrepha ludens* (Loew) (Darby and Kapp 1934). *D. crawfordi* failed to emerge at 12°C, while emergence for *A. ludens* at this temperature was 84%.

Mortality of *D. longicaudata* at low temperatures was greater for males than for females. The impact of male mortality on *D. longicaudata* populations would normally be minimal. However, very low male emergence could result in many females not mating and producing only male progeny (=constrained sex allocation, see Godfray 1994). Occurrence of this phenomenon over several consecutive generations could lead to extinction. This is, nonetheless, unlikely under field conditions, as no more than 1-2 consecutive generations would be exposed to sufficiently cold temperatures.

The common occurrence of arrested development at 15°C suggests that this species is somewhat adapted to periods of low temperatures. Low adult mortality and reduced ovipositional activity at low temperatures may be additional adaptations to cold conditions.

While there may be some immature parasitoid mortality as a direct effect of low temperatures, it is uncertain whether it is sufficient to explain the absence of *D. longicaudata* from large areas of the host range in central Florida (Chapter 3), or the low population levels following cold winters (Chapter 4). Loni (1997) concluded that temperature influence alone is insufficient to explain the absence of *P. concolor* at high latitudes in Italy. The differences in mean minimum winter temperatures between LaBelle, where *D. longicaudata* is common, and sites to the north where it is absent, are less than 2°C (Table 3-2). The variability among these towns in extreme minimum temperatures is similarly small. Thus small differences in temperature tolerances between the parasitoid and its host may account for absence of the parasitoid. However, it is difficult to relate studies of development in constant temperatures with the dynamic temperature fluctuations typical of field conditions. Extreme temperatures and their frequencies may be important determinants of mortality. Laboratory studies using variable temperature regimens to simulate field conditions are needed to better understand the relationships between temperature and distribution.

In order for direct temperature effect to explain the absence of *D. longicaudata*, this species must be less tolerant to low temperatures than *Doryctobracon areolatus* (Szepligeti). Therefore, experiments comparing the tolerances of both species are necessary. Unfortunately, difficulties with the maintenance of *D. areolatus* laboratory cultures have prevented such studies at the present time.

CHAPTER 6
LABORATORY REARING OF *DORYCTOBRACON AREOLATUS*

Doryctobracon areolatus (Szepligeti) is the dominant native parasitoid of *Anastrepha* spp. in many areas of the American tropics and subtropics (see references in Chapter 2). However, due to difficulty in rearing this species, it has not been utilized in augmentative release projects. Such releases have been limited to exotic parasitoids easily established in laboratory cultures such as *Diachasmimorpha longicaudata* (Ashmead) (Sivinski 1996). Other species of opiine braconids successfully reared on tephritid fruit flies in the laboratory include *Diachasmimorpha tryoni* (Cameron), *Fopius arisanus* (Sonan), *F. vandenboschi* (Fullaway) and *Psyttalia fletcheri* (Silvestri) (Ramadan et al. 1992, 1994b, 1995, Wong and Ramadan 1992).

A particularly important problem in rearing *D. areolatus* has been the dependence on fruits as rearing media for the host fly larvae. Chemical cues emanating from host fruits are apparently essential for host location in this species (Chapter 7). This chapter describes an efficient rearing method utilizing host fruit chemicals to stimulate oviposition into artificial units containing host larvae in diet.

Materials and Methods

Insects

Parent generation *D. areolatus*, a total of 128 females and 41 males, were reared out of guava fruits collected at LaBelle, Florida. Host Caribbean fruit fly, *Anastrepha*

suspensa (Loew), larvae were obtained from the mass-rearing facility, Florida Department of Agriculture and Consumer Services, Division of Plant Industry.

Cage Setup

Adult parasitoids were maintained in 20 cm^3 metal-framed cages, the top and two side panels with 16-mesh screens, and other panels Plexiglas. One of the side Plexiglas panels included a cloth sleeve. A brown paper towel was taped to the outside of the opposing Plexiglas panel, in order to cut down on the light intensity. Each cage was stocked over a period of several days (depending of the emergence rate) with approximately 100 females and 100 males. A total of 1, 2 and 5 cages were set up with parent, first and second generation parasitoids, respectively. Parasitoids were supplied daily with a fresh block of honey agar set on an inverted 30 ml plastic cup, and a strip of honey on the Plexiglas side panel, as food. A water dispenser constructed from a 100 ml plastic cup was placed in each cage.

Cages were maintained in a room at 25 ± 0.5°C, variable humidity and a 14:10 (L:D) hr photoperiod.

Exposure to Host Larvae

Oviposition units were composed of *A. suspensa* larvae in diet (Burns 1995) between two layers of cloth, topped with a layer of parafilm, all maintained within a 7.6 cm diameter plastic embroidery hoop. Prior to exposure, the parafilm had been wrapped overnight on a fresh Anjou pear, previously placed for several hours in a cage with adult *A. suspensa*. It was placed in the unit exposed side out. Each sheet of parafilm was used

on two consecutive days. Between exposures it was kept in a sealed and refrigerated plastic cup.

Approximately 40 cm^3 diet containing several hundred host larvae were placed in each oviposition unit. The larvae-diet mixture was selected from areas of the larval trays containing high densities of larvae, so that at least 50% of the volume was larvae. This was done in order increase the chance of successful probing by the parasitoids. The amount of diet placed in the unit was considered to be optimal. More diet would have made it too high, allowing larvae to migrate down and avoid parasitism. Less diet would have left parts of the unit devoid of hosts, thus decreasing the chance of a successful probing. Host larvae were usually 4 or 5 days old, corresponding to late second and/or early third instar. Occasionally 3 or 6 day old larvae were used.

The oviposition unit was placed upon an inverted 100 ml plastic cup. Parasitoids were exposed to hosts for ca. 8 hr daily. However, when high activity (15 or more parasitoids simultaneously on the oviposition unit) was observed, two successive exposures were performed, with units being replaced after 4 hr. This was done in order to reduce the chance of superparasitism.

Parasitoids were first exposed to hosts within several days of emergence. Exposure continued daily, depending on availability of suitable hosts.

Immature Stages and Adult Emergence

Upon completion of exposure, host larvae were transferred to 30 ml plastic cups, which were filled to the top with fresh diet. These cups were then placed upon moist fine vermiculite (15-20 ml water per 100 cm^3 vermiculite) in 500 ml plastic cups. Fully developed larvae emerged from the diet, dropping to the vermiculite in which they

pupated. After allowing larvae to emerge for several days, the vermiculite was sieved, and host puparia transferred into fresh moist vermiculite within 100 ml plastic cups. These cups were covered with a solid lid, which was replaced after one week with a cloth lid. This procedure allowed the vermiculite to remain moist while minimizing development of fungi. Immature stages were maintained at the same environmental conditions as adults.

Adult parasitoid emergence was recorded daily, and parasitoids transferred to screened cages. Cups were discarded when no emergence was observed for several days.

Life History Traits

Because cages were stocked over several days, the exact age of ovipositing females could not be determined. Age was estimated as the difference between the exposure date and the median emergence date of all females in the cage. This age estimate was subsequently related with progeny production and sex ratio. Only second-generation cages were used in these calculations.

At the end of the experiment, the total number of females found dead was only 66 and 65% of the number put in the cages for the first and second generations, respectively. This suggests that a large number of parasitoids escaped. Indeed, some parasitoids were observed pushing through holes in the screen on the top panel of the cage. However, it was assumed that most escaped shortly after being put into the cages, and did not significantly contribute to progeny production. Therefore, the number of females in a cage on a given date was estimated by subtracting the number dying from that day forward from the total dying in the cage.

Results and Discussion

Total production and sex ratio of progeny for the three generations are shown in Figure 6-1. Progeny production was very low for the parent generation, with only 2.4 progeny per female. However, the laboratory-reared females produced larger numbers. Production for the first and second generations was 12.1 and 9.3 progeny per female, respectively. This is still much lower than the 29.6 progeny per female reported for *D. longicaudata* (Greany et al. 1976). Note that the rearing methods differed between these studies, so that this may not be a representative comparison of the reproductive potentials of the two species.

The sex ratio of second-generation progeny was highly male-biased (Figure 6-1). Note that these were progeny from females in a single first-generation cage. A similar phenomenon was observed in the progeny of females from a single cage in a previous rearing project. The male-biased sex ratio may be the result of many females not having mated. The cause of this is unclear.

Mean daily progeny production was between 1-2 progeny per female for almost all days from age 9 to 22 days (Figure 6-2). In contrast, daily progeny production for *D. longicaudata* was shown to peak at nearly 4 progeny per female, but remained above one progeny per female for only 9 consecutive days (Greany et al. 1976). Note that for both species the number of mature eggs in the ovaries (*D. areolatus*, 64.3 ± 4.3, n=6; *D. longicaudata*, 73.0 ± 6.3, n=6; t=1.18, p=0.26; 7-day-old females not exposed to hosts, specimens obtained from Martin Aluja, Instituto de Ecologia, Xalapa, Veracruz, Mexico) is much greater than the maximum number oviposited per day. The differences in progeny production may be the result of different experimental procedures or differential

adaptability to laboratory conditions. However, they may also represent different reproductive strategies, whereby *D. longicaudata* produces large numbers of progeny in a short period of time, and *D. areolatus* smaller numbers over longer periods. If this were the case, it would give young *D. longicaudata* females a competitive advantage in exploiting host patches (see discussion in Chapter 3).

The sex ratio of progeny of second-generation females was relatively stable over time, averaging close to 50% (Figure 6-3). However, at the oldest female ages the progeny sex ratio tended to be male-biased. This may be the result of sperm depletion, or perhaps lower mortality of unmated females.

Immature development time at 25°C was 22.1 ± 1.1 days (range 19-35 days) for females and 20.6 ± 1.1 days (range 18-26 days) for males.

The rearing method reported here is a vast improvement over the previously used method of rearing on hosts within fruits. While production numbers are lower and costs higher than with *D. longicaudata*, this method could still serve as a basis for establishment of laboratory cultures for research. Further improvements in rearing techniques could make possible mass-production for purposes such as augmentative releases. Chemical identification of fruit cues used for host location might totally eliminate the need for fruits. Improvements in nutrition and control of pathogens would also be beneficial. Other improvements including smaller mesh screens to prevent escape and differently designed cages with more surface area for resting have already been implemented in subsequent studies (see Chapter 7).

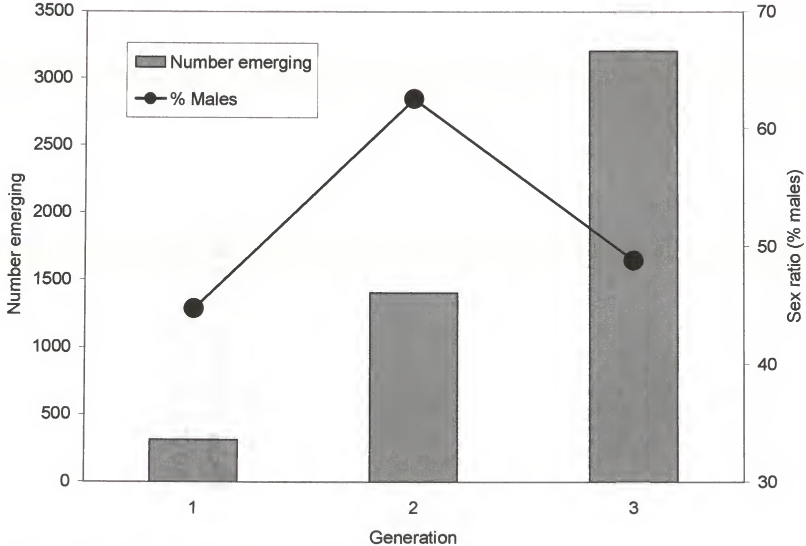

Figure 6-1. Total numbers and sex ratio of emerging *Doryctobracon areolatus*.

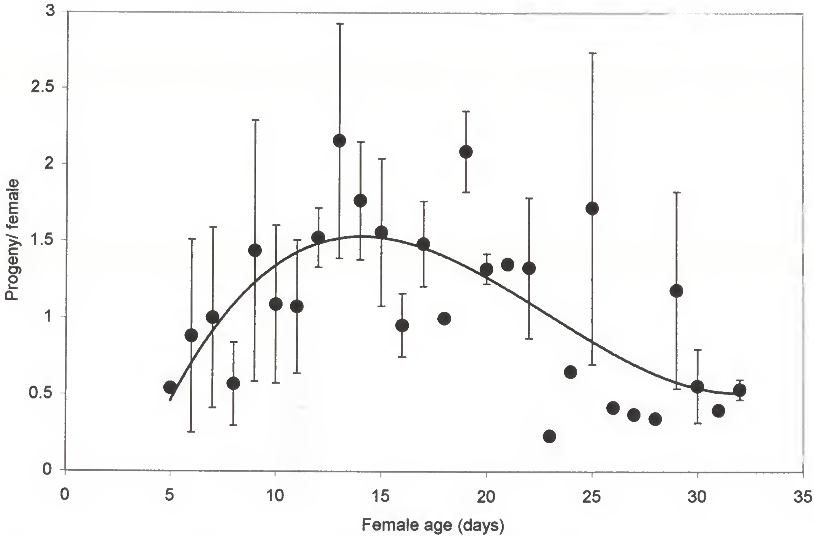

Figure 6-2. Daily progeny production by second-generation *Doryctobracon areolatus* females.

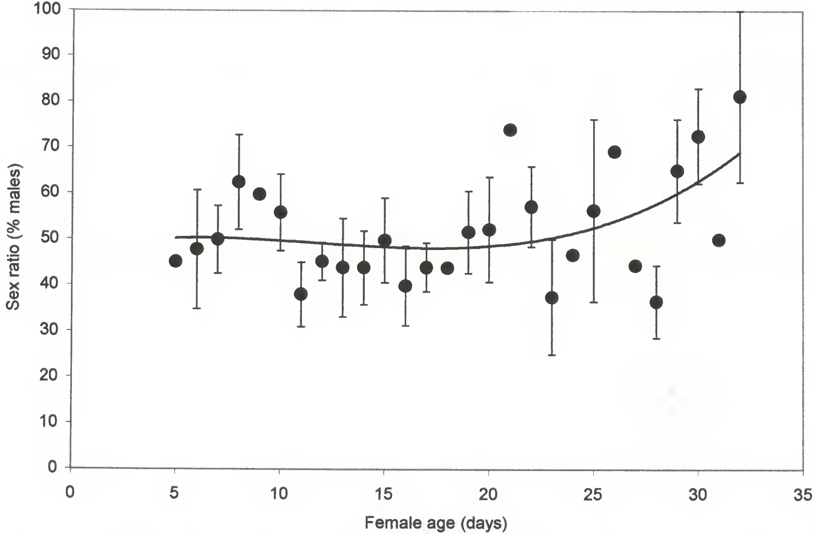

Figure 6-3. Relationship between age of second-generation *Doryctobracon areolatus* females and sex ratio of progeny produced.

CHAPTER 7
BEHAVIORAL RESPONSE TO HOST CHEMICAL CUES BY FEMALES OF *DORYCTOBRACON AREOLATUS*

Diachasmimorpha longicaudata (Ashmead) locates hosts within fruits by sensing the vibrations of the moving larvae (Lawrence 1981). Females of this species respond to an artificial apparatus containing host larvae with immediate landing, probing and oviposition. In contrast, *Doryctobracon areolatus* (Szepligeti) females show no such response. However, if a sheet of parafilm previously wrapped on a fruit exposed to flies is incorporated into this apparatus, flight to the device and oviposition response is observed. This suggests that host chemical cues are essential in the host location behavior of *D. areolatus*.

Chemical cues are important facilitators of host location in many parasitoids. These may be associated with either the host insect or with the plant on which it feeds (Godfray 1994). This study is designed to determine the source of the host cues utilized by *D. areolatus*, i.e. whether they are associated with the host fly or fruit.

Materials and Methods

Insects

Adult *Doryctobracon areolatus* were from a third-generation laboratory culture, the parent generation of which was reared from Cattley guava (*Psidium cattleianum* Sabine) fruit collected mostly at LaBelle, Florida. Caribbean fruit fly, *Anastrepha*

suspensa (Loew), larvae were obtained from the laboratory colony maintained for ca. 150 generations at the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, Florida.

Experimental Design

Cages were 30 cm long x 20 cm wide x 20 cm high. The bottom and two longer sides were Plexiglas, with a cloth sleeve in the middle of one of the side panels. The top panel was 52-mesh screen, and the two smaller sides 16-mesh screen. Each of 6 cages was stocked with 100 female and 70 male *D. areolatus*. Dead females were replaced daily.

Oviposition units were composed of several hundred second and/or third instar *A. suspensa* larvae in diet (Burns 1995) between two layers of cloth, topped with a layer of parafilm, all maintained within a 7.6 cm diameter wooden embroidery hoop.

Two oviposition units were placed in each cage upon plastic containers. One unit ("Control") contained parafilm wrapped overnight on unwaxed Anjou pears exposed to ovipositing *A. suspensa* females for several hours. This was identical to the units used in rearing the laboratory culture (Chapter 6). The second unit contained parafilm with one of the following treatments: (1) "Unpunctured fruit"- wrapped on fresh undamaged pear; (2) "Punctured fruit"- wrapped on pear punctured approximately 200x with a no. 0 insect pin (to simulate puncturing by ovipositing flies); (3) "Damaged fruit"- wrapped on pear from which sections of pulp had been cut out (to simulate vertebrate damage); (4) "Fly cues"- placed for several hours within cage containing ovipositing *A. suspensa* females (flies oviposited through the parafilm between several to several hundred times); (5) "Fly cues

+ punctured fruit"- as treatment (4) but subsequently wrapped on punctured pear; (6) Untreated parafilm.

Previous observations indicated that naïve individuals (without oviposition experience) showed relatively little response to the oviposition unit. Therefore, prior to experimentation, females were exposed to a control oviposition unit at least once. The experiment was replicated on 12 of 13 consecutive days. On each day, each of the 6 cages contained a different treatment. Each treatment was replicated twice in each cage, once placed on the left side and once on the right side of the cage. The placement on any given day was random.

Exposure to each pair of oviposition units lasted 8-10 hr. Fruit fly larvae were transferred to a small plastic container, which was filled with fresh diet. This container was placed within a larger container with moist fine vermiculite (15-20 ml water per 100 cm^3 vermiculite). Mature larvae exited the diet and pupated in the vermiculite. Containers with vermiculite were covered with a solid lid for one week, and subsequently with a screened lid until parasitoid emergence.

Response Variables and Statistical Analysis

The number of females active on each oviposition unit was recorded at 1 hr, 4 hr, and 8 hr following placement of the units in the cage. An active female was defined as an individual either probing into the unit with its ovipositor, or one standing on the unit with ovipositor at a horizontal or below horizontal position; otherwise the ovipositor is curved slightly upward. The difference between the "Control" and "Treatment" units was calculated for each cage at each hour. The number of *D. areolatus* progeny from each

oviposition unit was counted, and the difference between the "Control" and "Treatment" units calculated for each cage. Treatments were compared by paired t-test.

Results

The unpunctured and punctured fruit treatments did not differ from the control (fruit exposed to flies) in terms of number of active *D. areolatus* females on the oviposition unit (t=1.77, p=0.08; t=0.26, p=0.80; respectively). The fly cues + punctured fruit, damaged fruit, fly cues, and untreated parafilm treatments all showed less response than the control (t=2.24, p=0.03; t=3.83, p=0.0003; t=7.28, p=0.0001; t=6.80, p=0.0001; respectively). Figure 7-1 compares the response of females among the various treatments. All of the fruit treatments showed significantly greater response that either fly cues or untreated parafilm. Additionally, response to punctured fruit odor was greater than that to odor of damaged fruit.

In the fly cues + unpunctured fruit treatment, there was a significant reduction in the number of females on the oviposition unit after 8 hr, as compared to both 1 hr and 4 hr (t=4.23. p=0.0001; t=2.43, p=0.01; respectively). Consequently, there was a significantly lesser response after 8 hr to this treatment than to either the unpunctured or punctured fruit treatments (t=2.50, p=0.04; t=3.67, p=0.002; respectively). The cause of this is unclear.

The number of progeny emerging from the unpunctured fruit, punctured fruit and fly cues + punctured fruit treatments was not significantly different than the number emerging from the control units (t=0.07, p=0.94; t=1.48, p=0.14; t=2.24, p=0.03; respectively). Progeny emergence from the damaged fruit, fly cues and untreated parafilm treatments was significantly lower than from the control units (t=2.66, p=0.01;

t=4.67, p=0.0001; t=5.00, p=0.0001; respectively). Figure 7-2 compares the emergence among the various treatments. Emergence from the fly cues and untreated parafilm treatments was significantly lower than from all fruit treatments except damaged fruit. There were no significant differences in emergence among fruit treatments.

Discussion

Several studies have demonstrated the importance of host-associated chemicals in host location by parasitoids of fruit flies. Greany et al. (1977) found that chemicals released by fungi associated with rotten fruits are attractive to *D. longicaudata* females. Messing and Jang (1992), using chopped ripe fruits placed in traps, demonstrated attraction of *D. longicaudata* females to various host fruits. Messing et al. (1996) demonstrated similar responses by *Psyttalia fletcheri* (Silvestri) to odors of fresh cucumber and decaying pumpkin. These studies measured adult attraction and only infer that this response is related to oviposition. The current study differs in that the response variables directly measure ovipositional activity.

This study clearly demonstrates the importance of chemical cues emanating from ripe host fruit in the host location behavior of *D. areolatus*. Response to unpunctured fruit did not differ from that to punctured fruit. This suggests that response is unrelated to host fly ovipositional activity, which the puncturing was designed to simulate. Response to damaged fruit was somewhat less than to the other fruit treatments. As the peel was removed and the pulp exposed in this treatment, this suggests that the active chemical(s) may be located in the peel of the fruit.

The bioassay used in this study could not determine if the fruit chemical(s) act as attractants, arrestants, or oviposition stimulants, or if they are volatile or contact

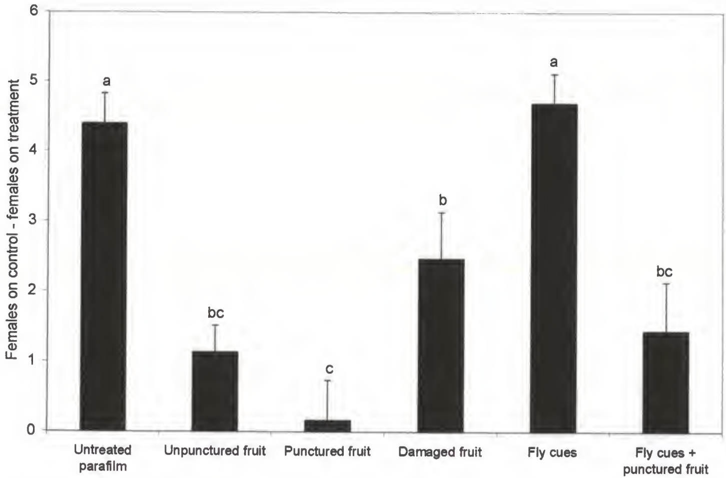

Figure 7-1. Difference between the number of *Doryctobracon areolatus* females on the control oviposition unit (cues from fruit exposed to flies) and the number of females on oviposition units treated with chemical cues from various sources. Larger differences imply lesser response to the treatment units. Bars with the same letter are not significantly different, $p = 0.05$ according to paired t-test, with hourly observations treated as repeated measurements.

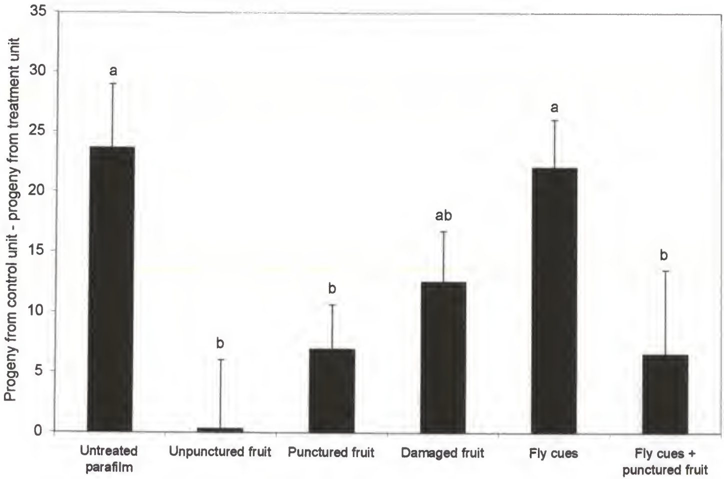

Figure 7-2. Difference between the number of *Doryctobracon areolatus* progeny from the control oviposition unit (cues from fruit exposed to flies) and the number of progeny from oviposition units treated with chemical cues from various sources. Larger differences imply lesser response to the treatment units. Bars with the same letter are not significantly different, p=0.05 according to paired t-test.

chemicals. More than one class of chemicals may be involved, or one chemical may have a role in successive stages of the host-location behavior. Females have been observed landing on the periphery of the oviposition unit, and walking onto the parafilm while antennating. This behavior suggests that volatile fruit chemicals may be at least partially involved in host location.

Prokopy and Webster (1978) found that *Utetes canaliculatus* (=*Opius lectus*) (Gahan) responds primarily to the host-marking pheromone of *Rhagoletis pomonella* (Walsh). Similarly, *Halticoptera rosae* Burks (Hymenoptera: Pteromalidae) was found to respond to the pheromone deposited by *Rhalogelis basiola* (Osten Sacken) (Roitberg and Lalonde 1991). Chemical cues derived from the host fly have no apparent effect on *D. areolatus* females. While both *U. canaliculatus* and *H. rosae* parasitize eggs or early-instar larvae, *D. areolatus* prefers later instars (Chapter 6). As the host pheromone is water-soluble, it would be degraded by precipitation. Thus the former two species, which attack the host shortly following oviposition, should conceivably have a closer association with it, and more likely evolve a response.

D. longicaudata can locate larvae within fruit solely by vibration sensing (Lawrence 1981). Vibrotaxis has also been reported for *Diachasmimorpha mellea* (Gahan) (Lathrop and Newton 1933), *Diachasma alloeum* (Muesebeck) (Glas and Vet 1983), and *Aganaspis pelleranoi* (Brethes) (Hymenoptera: Eucoilidae) (Ovruski 1994). Henneman (1996) demonstrated that *Diachasmimorpha juglandis* (Muesebeck) females discriminate between infested and uninfested walnut fruits before landing, but did not determine which cues may be involved. *D. areolatus* requires chemical cues associated with the fruit for host location. However, this does not imply that vibration cues are not

used by this species. Chemical cues may be used in the early stages of host location, as attractants or arrestants, with vibration stimulating probing behavior once the parasitoid is on the fruit.

The greater dependence of *D. areolatus* on host fruit odors relative to *D. longicaudata* suggests a greater affinity to these odors, and perhaps an advantage in locating host patches. Distribution patterns of these two species in the field are consistent with *D. areolatus* being superior to *D. longicaudata* in this regard (Chapters 3 and 4, Sivinski et al. 1998).

CHAPTER 8
SUMMARY AND CONCLUSIONS

Two main trends were observed in the distribution of Caribbean fruit fly (*Anastrepha suspensa* (Loew)) parasitoids in Florida (Chapter 3). First, *D. longicaudata* was absent from a large area of interior central Florida, north of the towns of LaBelle and Okeechobee. Second, *D. areolatus* was absent from the Atlantic coast and rare on the coast of the Gulf of Mexico.

Populations of both *D. longicaudata* and *D. areolatus* are reduced following cold winters. Nevertheless, *D. longicaudata* is more adversely affected (Chapter 4). Similarly, the geographic region in which *D. longicaudata* is absent is characterized by low winter temperatures. However, absence of *D. longicaudata* is best explained by high variability in temperatures.

Two hypotheses are proposed to explain the effect of temperature on *D. longicaudata*: (1) Low temperatures have a direct negative effect. (2) Low or variable temperatures result in periods of low host availability, and such temporal gaps in hosts are detrimental to *D. longicaudata* survival. Field data from Florida are generally consistent with both hypotheses.

Laboratory studies using constant temperature regimens suggest that *D. longicaudata* is somewhat less tolerant to low temperatures than is the host *A. suspensa* (Chapter 5). However, it is unclear whether this difference is sufficient to explain absence of the parasitoid from large regions of the host's range. Additionally, the phenomenon of

delayed emergence of *D. longicaudata* at low temperatures suggests a certain adaptation to these conditions.

Several lines of evidence support the hypothesis of an indirect temperature effect on *D. longicaudata* distribution. First, variances of monthly temperatures, rather than absolute temperatures, are the most significant variables related with presence at a certain site. Variability of temperature among months is a measure of seasonality, and is likely to be related with host availability. Furthermore, a positive relationship was observed between *D. longicaudata* abundance and numbers of host flies captured in traps at various sites, while no such relationship was found for *D. areolatus*. This suggests that *D. longicaudata* is less successful under conditions of low host density. Such conditions would be more frequent at locations with greater seasonal fluctuations in temperature.

The rare occurrence of *D. areolatus* along the coasts, and especially its absence in the area of its original introduction, may be the result of interspecific competition. There is little overlap in distribution with *D. longicaudata*, which was introduced three years later. Of all the sites surveyed, only at LaBelle do both species co-occur in large numbers. Studies at LaBelle suggest that significant competition may occur at least at the end of the Surinam cherry fruiting season (Chapter 4). The negative among-site relationship in abundance between *D. areolatus* and *U. anastrephae* (Chapter 3) may also be indicative of competition.

Distribution patterns at LaBelle are consistent with "counter-balanced competition" (cf. Zwölfer 1971) where *D. areolatus* is superior to *D. longicaudata* in locating host patches (=extrinsic competitor) and *D. longicaudata* is superior in exploiting these patches (=intrinsic competitor) (Chapter 4, Sivinski et al. 1998). Host

fruit chemicals are important cues in the host location behavior of *D. areolatus*, and are apparently essential for stimulating oviposition in the laboratory (Chapters 6 and 7). This may be related to its ability to locate host patches. Conversely, *D. longicaudata* does not require fruit cues to locate host larvae in the laboratory, and it has been shown to locate hosts within fruits using vibration cues (Lawrence 1981). This may be related to its ability to exploit host patches. Note that attraction to fresh host fruit chemicals has been shown for *D. longicaudata* in the field, and it is unclear whether *D. areolatus* can detect vibrations of host larvae. Further studies comparing these two species are needed to resolve how they may be differ in host and host-habitat location strategies.

Several additional mechanisms may contributed to a competitive advantage for *D. longicaudata* over *D. areolatus*. Perhaps the most obvious is its longer ovipositor, which enables it to reach host larvae deeper within the fruit. Comparisons of laboratory studies suggest that *D. longicaudata* females may lay larger numbers of eggs during the first days of adult life (Chapter 6, Greany et al. 1976). If this is representative of behavior in the field (which is far from certain), it would enable faster exploitation of host patches.

Finally, studies have indicated that at least under certain circumstances, *D. longicaudata* larvae may have an advantage in physical competition with other parasitoid species within host larvae (see references in Chapter 3). Further studies are needed to determine whether such an advantage exists over *D. areolatus* larvae.

APPENDIX

NUMBERS OF SAMPLES COLLECTED AND INSECTS EMERGING FOR VARIOUS SITES BY MONTH, YEAR AND FRUIT TYPE

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Arcadia	August	1994	Common guava	3	3	3	0	0	375	54	0	0
	January	1995	Loquat	8	8	1	0	0	197	8	0	0
	February	1995	Loquat	8	8	2	0	0	293	25	0	0
	March	1995	Loquat	10	10	7	0	0	987	137	0	0
	April	1995	Loquat	9	9	3	0	0	321	38	0	0
	May	1995	Surinam cherry	3	2	2	0	1	41	108	0	3
	June	1995	Surinam cherry	7	7	2	0	0	212	58	0	0
	July	1995	Surinam cherry	1	0	0	0	0	0	0	0	0
			Cattley guava	2	2	2	0	0	60	128	0	0
	August	1995	Cattley guava	1	1	1	0	0	0	6	0	0
			Common guava	4	4	3	0	0	274	17	0	0
	September	1995	Common guava	3	3	1	0	0	335	10	0	0
Belle Glade	August	1994	Common guava	10	10	0	1	0	705	0	21	0
	January	1995	Surinam cherry	3	3	0	0	0	213	0	0	0

[a] CFF = Caribbean fruit fly.

[b] Da = *Doryctobracon areolatus.*

[c] Dl = *Diachasmimorpha longicaudata.*

[d] Ua = *Utetes anastrephae.*

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Belle Glade	January	1995	Cattley guava	1	0	0	0	0	0	0	0	0
			Common guava	3	3	0	0	0	708	0	0	0
	February	1995	Loquat	1	1	0	0	0	4	0	0	0
			Surinam cherry	1	1	0	0	0	0	0	0	0
			Common guava	3	3	0	1	0	127	0	1	0
	March	1995	Loquat	5	3	0	0	0	25	0	0	0
			Surinam cherry	4	3	0	2	1	105	0	26	4
			Common guava	2	2	0	1	0	132	0	1	0
	April	1995	Loquat	2	2	0	0	0	47	0	0	0
			Surinam cherry	6	5	0	3	1	240	0	14	2
			Common guava	1	1	0	0	0	15	0	0	0
	May	1995	Surinam cherry	7	7	0	7	4	41	0	23	17
			Common guava	1	1	0	0	0	19	0	0	0
	July	1995	Surinam cherry	5	4	0	0	1	95	0	0	1
			Common guava	3	3	0	2	0	496	0	13	0
	August	1995	Surinam cherry	3	3	0	0	2	25	0	0	3
			Common guava	1	1	0	1	0	17	0	1	0
	September	1995	Surinam cherry	2	1	0	0	0	12	0	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Belle Glade	September	1995	Common guava	7	6	0	2	0	436	0	6	0
Bradenton	August	1994	Common guava	1	1	0	0	0	12	0	0	0
	January	1995	Loquat	1	1	0	0	0	16	0	0	0
	February	1995	Loquat	8	6	0	0	0	72	0	0	0
			Cattley guava	1	0	0	0	0	0	0	0	0
			Common guava	1	0	0	0	0	0	0	0	0
	March	1995	Loquat	10	7	0	0	1	170	0	0	1
	April	1995	Surinam cherry	1	1	0	0	0	51	0	0	0
	August	1995	Surinam cherry	1	1	0	0	0	5	0	0	0
			Common guava	5	4	0	0	0	126	0	0	0
	September	1995	Surinam cherry	1	1	0	0	0	4	0	0	0
	March	1996	Loquat	10	3	0	0	0	62	0	0	0
	April	1996	Loquat	3	2	0	0	0	111	0	0	0
			Surinam cherry	9	9	0	0	0	571	0	0	0
	May	1996	Surinam cherry	12	12	0	1	3	616	0	6	32
Dade City	August	1994	Common guava	5	4	0	0	0	155	0	0	0
	January	1995	Loquat	7	6	0	0	0	40	0	0	0
	February	1995	Loquat	10	8	0	0	0	59	0	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Dade City	March	1995	Loquat	10	10	0	0	0	237	0	0	0
	April	1995	Loquat	2	2	0	0	0	71	0	0	0
	August	1995	Common guava	1	1	0	0	0	63	0	0	0
	September	1995	Common guava	1	1	0	0	0	47	0	0	0
Ft. Lauderdale	August	1994	Common guava	8	8	0	3	1	633	0	24	2
	January	1995	Surinam cherry	8	7	0	0	0	400	0	0	0
			Common guava	1	1	0	0	0	62	0	0	0
	February	1995	Loquat	3	2	0	0	0	104	0	0	0
			Surinam cherry	6	6	0	0	1	270	0	0	3
	March	1995	Loquat	6	5	0	1	1	235	0	12	4
			Surinam cherry	4	4	0	2	2	184	0	129	25
	April	1995	Surinam cherry	7	6	0	1	2	236	0	3	14
	May	1995	Surinam cherry	5	3	0	3	2	42	0	21	11
	July	1995	Cattley guava	2	2	0	0	0	81	0	0	0
	August	1995	Common guava	4	4	0	2	0	499	0	25	0
Ft. Myers	August	1994	Cattley guava	3	2	1	1	0	195	16	38	0
			Common guava	1	1	0	1	0	80	0	5	0
	January	1995	Loquat	2	2	1	0	0	77	2	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Ft. Myers	February	1995	Loquat	8	7	0	2	0	164	0	8	0
	March	1995	Loquat	10	10	1	2	4	837	1	7	5
	April	1995	Loquat	7	5	0	3	2	191	0	26	10
			Surinam cherry	3	3	0	0	2	213	0	0	39
	May	1995	Surinam cherry	5	5	1	3	4	107	2	7	15
	June	1995	Surinam cherry	6	3	0	0	1	39	0	0	1
			Cattley guava	1	1	0	0	0	169	0	0	0
			Common guava	2	2	1	2	2	150	1	14	4
	July	1995	Cattley guava	10	10	3	5	3	713	4	42	4
	August	1995	Cattley guava	8	8	1	3	1	157	1	9	1
Ft. Pierce	March	1993	Loquat	6	6	0	2	2	364	0	3	49
			Surinam cherry	6	6	0	2	3	520	0	4	9
			Common guava	1	1	0	1	0	234	0	1	0
	May	1993	Surinam cherry	4	4	0	2	3	234	0	2	62
Haines City	January	1995	Loquat	7	3	0	0	0	28	0	0	0
	February	1995	Loquat	7	4	0	0	0	29	0	0	0
	March	1995	Loquat	6	5	0	0	0	167	0	0	0
	April	1995	Loquat	2	2	0	0	0	28	0	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Haines City	April	1995	Surinam cherry	1	0	0	0	0	0	0	0	0
	May	1995	Surinam cherry	3	1	0	0	0	8	0	0	0
	June	1995	Surinam cherry	3	3	1	0	0	21	1	0	0
	July	1995	Surinam cherry	2	0	0	0	0	0	0	0	0
LaBelle	August	1994	Common guava	11	10	5	5	0	569	144	52	0
	January	1995	Loquat	10	9	2	3	0	230	57	8	0
	February	1995	Loquat	11	11	2	4	0	249	28	19	0
	March	1995	Loquat	12	12	5	6	0	564	114	196	0
	April	1995	Loquat	6	6	2	4	0	143	11	89	0
			Surinam cherry	4	4	1	1	0	168	49	1	0
	May	1995	Surinam cherry	10	10	10	6	2	71	177	49	7
	June	1995	Surinam cherry	10	10	7	8	0	247	142	41	0
	July	1995	Surinam cherry	3	2	0	1	0	22	0	2	0
			Cattley guava	3	2	2	1	0	130	14	14	0
			Common guava	2	1	1	0	0	34	4	0	0
	August	1995	Cattley guava	2	2	1	1	0	13	14	2	0
			Common guava	8	7	2	1	0	338	6	1	0
	September	1995	Surinam cherry	1	0	0	0	0	0	0	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
LaBelle	September	1995	Common guava	10	9	2	2	0	489	8	8	0
Lakeland	August	1994	Common guava	10	10	3	0	0	1531	8	0	0
	January	1995	Loquat	8	3	0	0	0	6	0	0	0
	February	1995	Loquat	10	7	0	0	0	40	0	0	0
	March	1995	Loquat	10	7	0	0	0	127	0	0	0
	April	1995	Loquat	7	4	0	0	0	62	0	0	0
			Surinam cherry	3	3	1	0	0	64	5	0	0
	May	1995	Surinam cherry	5	4	2	0	0	136	9	0	0
	June	1995	Surinam cherry	8	6	2	0	0	131	6	0	0
	August	1995	Cattley guava	4	3	1	0	0	94	5	0	0
			Common guava	6	6	2	0	0	793	29	0	0
	September	1995	Common guava	10	0	2	0	1	645	110	0	2
Lake Placid	August	1994	Common guava	2	2	1	0	0	97	1	0	0
	January	1995	Loquat	9	8	1	0	0	146	1	0	0
	February	1995	Loquat	10	10	0	0	0	112	0	0	0
	March	1995	Loquat	10	9	3	0	0	500	13	0	0
	April	1995	Loquat	8	8	2	0	0	160	16	0	0
	May	1995	Surinam cherry	11	10	6	0	0	301	79	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Lake Placid	June	1995	Surinam cherry	8	8	3	0	1	236	17	0	1
	July	1995	Cattley guava	3	1	1	0	0	55	106	0	0
	August	1995	Common guava	5	5	4	0	0	1004	76	0	0
	September	1995	Common guava	4	4	2	0	0	226	17	0	0
Lake Wales	August	1994	Common guava	10	9	4	0	0	392	75	0	0
	February	1995	Loquat	10	9	2	0	0	301	17	0	0
	March	1995	Loquat	9	9	2	0	0	328	9	0	0
	April	1995	Loquat	2	2	0	0	0	123	0	0	0
			Surinam cherry	8	8	3	0	0	234	83	0	0
	May	1995	Surinam cherry	5	4	1	0	0	121	2	0	0
	June	1995	Surinam cherry	5	5	2	0	0	225	17	0	0
	August	1995	Common guava	9	6	3	0	0	341	11	0	0
	September	1995	Common guava	10	7	2	0	0	435	16	0	0
Melbourne	January	1995	Loquat	4	1	0	0	0	11	0	0	0
	February	1995	Loquat	10	4	0	0	0	21	0	0	0
	March	1995	Loquat	9	3	0	0	0	16	0	0	0
			Surinam cherry	1	0	0	0	0	0	0	0	0
	May	1995	Surinam cherry	10	9	0	0	0	72	0	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Melbourne	July	1995	Surinam cherry	1	1	0	0	0	10	0	0	0
	August	1995	Surinam cherry	1	1	0	0	0	8	0	0	0
			Cattley guava	3	2	0	0	0	3	0	0	0
			Common guava	7	3	0	0	0	76	0	0	0
	September	1995	Surinam cherry	1	1	0	0	0	4	0	0	0
			Cattley guava	1	0	0	0	0	0	0	0	0
			Common guava	11	7	0	0	0	133	0	0	0
	March	1996	Loquat	10	7	0	0	0	56	0	0	0
	April	1996	Loquat	8	8	0	0	0	278	0	0	0
			Surinam cherry	3	1	0	0	0	5	0	0	0
	May	1996	Loquat	1	1	0	0	0	32	0	0	0
			Surinam cherry	4	4	0	0	0	236	0	0	0
Miami	August	1994	Common guava	10	9	0	1	0	435	0	17	0
	January	1995	Loquat	1	1	0	1	1	51	0	2	2
	February	1995	Loquat	1	0	0	0	0	0	0	0	0
			Surinam cherry	2	2	0	0	0	35	0	0	0
			Common guava	1	1	0	0	0	64	0	0	0
	March	1995	Loquat	1	1	0	0	0	33	0	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Miami	April	1995	Surinam cherry	3	1	0	0	0	26	0	0	0
	May	1995	Surinam cherry	5	5	0	3	0	93	0	7	0
	June	1995	Surinam cherry	2	2	0	2	2	69	0	39	7
	July	1995	Cattley guava	1	1	0	0	1	4	0	0	1
	August	1995	Cattley guava	1	1	0	0	0	36	0	0	0
			Common guava	12	9	0	1	0	1336	0	4	0
	September	1995	Common guava	8	7	0	3	0	357	0	12	0
Naples	August	1994	Common guava	10	5	0	1	0	28	0	4	0
	January	1995	Loquat	1	0	0	0	0	0	0	0	0
			Cattley guava	4	2	0	0	0	26	0	0	0
	February	1995	Loquat	9	3	0	0	0	26	0	0	0
	March	1995	Loquat	10	8	0	0	1	95	0	0	1
	April	1995	Loquat	6	6	0	1	0	313	0	1	0
			Surinam cherry	4	2	0	1	0	37	0	1	0
	May	1995	Surinam cherry	9	6	0	0	1	78	0	0	1
	June	1995	Surinam cherry	10	7	1	2	2	202	4	23	6
	July	1995	Cattley guava	9	3	0	0	0	77	0	0	0
	August	1995	Cattley guava	10	9	1	4	2	328	1	29	28

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Naples	September	1995	Cattley guava	1	0	0	0	0	0	0	0	0
Okeechobee	September	1994	Common guava	3	1	0	0	0	107	0	0	0
	January	1995	Loquat	2	1	0	0	0	2	0	0	0
			Surinam cherry	1	1	1	1	0	39	39	1	0
			Common guava	2	2	0	1	0	106	0	1	0
	February	1995	Loquat	1	0	0	0	0	0	0	0	0
			Surinam cherry	1	0	0	0	0	0	0	0	0
	March	1995	Loquat	2	2	0	0	0	30	0	0	0
			Surinam cherry	1	1	1	1	0	20	23	6	0
			Common guava	1	1	0	0	0	54	0	0	0
	April	1995	Loquat	1	1	0	0	0	1	0	0	0
			Surinam cherry	1	1	0	0	0	60	0	0	0
	September	1995	Surinam cherry	1	1	0	0	0	1	0	0	0
			Common guava	1	0	0	0	0	0	0	0	0
	March	1996	Loquat	10	9	0	0	0	161	0	0	0
	April	1996	Loquat	5	5	0	0	0	92	0	0	0
			Surinam cherry	5	4	0	0	0	265	0	0	0
	May	1996	Surinam cherry	10	10	4	1	1	810	119	1	7

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Punta Gorda	February	1995	Loquat	10	5	0	0	0	194	0	0	0
	March	1995	Loquat	8	8	1	0	0	502	8	0	0
			Surinam cherry	2	2	0	0	0	259	0	0	0
	April	1995	Loquat	7	2	0	0	0	107	0	0	0
			Surinam cherry	1	1	0	0	1	30	0	0	3
	May	1995	Surinam cherry	1	1	1	0	0	12	8	0	0
	June	1995	Surinam cherry	10	8	2	0	2	218	2	0	8
	July	1995	Surinam cherry	2	1	0	0	0	7	0	0	0
			Cattley guava	3	3	1	1	0	108	1	1	0
	August	1995	Surinam cherry	3	1	0	0	0	9	0	0	0
			Cattley guava	7	4	0	0	0	33	0	0	0
St. Cloud	August	1994	Common guava	8	5	0	0	0	300	0	0	0
	January	1995	Loquat	3	0	0	0	0	0	0	0	0
	February	1995	Loquat	3	0	0	0	0	0	0	0	0
	March	1995	Loquat	3	1	0	0	0	1	0	0	0
	April	1995	Loquat	3	2	0	0	0	4	0	0	0
	May	1995	Surinam cherry	7	6	0	0	0	110	0	0	0
	June	1995	Surinam cherry	7	6	0	0	0	142	0	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
St. Cloud	July	1995	Surinam cherry	2	2	0	0	2	40	0	0	16
	August	1995	Common guava	10	9	0	0	0	582	0	0	0
	September	1995	Common guava	5	5	0	0	0	109	0	0	0
St. Petersburg	August	1994	Common guava	6	6	0	0	0	699	0	0	0
	January	1995	Loquat	5	4	0	0	0	8	0	0	0
	February	1995	Loquat	10	0	0	0	0	0	0	0	0
	March	1995	Loquat	10	5	0	0	0	35	0	0	0
			Common guava	2	2	0	0	0	27	0	0	0
	April	1995	Loquat	4	4	0	0	0	60	0	0	0
			Surinam cherry	1	1	0	0	0	0	0	0	0
			Common guava	2	2	0	0	0	25	0	0	0
	May	1996	Surinam cherry	10	10	0	0	0	500	0	0	0
Tampa	August	1994	Common guava	8	8	1	0	0	727	1	0	0
	January	1995	Loquat	9	3	0	0	0	28	0	0	0
	February	1995	Loquat	10	7	0	0	0	53	0	0	0
	March	1995	Loquat	9	9	1	0	0	390	1	0	0
Venice	February	1995	Loquat	5	5	0	0	0	63	0	0	0
	March	1995	Loquat	5	3	0	0	0	241	0	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
Venice	April	1995	Surinam cherry	5	5	0	0	2	518	0	0	6
	June	1995	Surinam cherry	5	5	0	0	3	265	0	0	6
	March	1996	Loquat	2	0	0	0	0	0	0	0	0
	April	1996	Loquat	3	3	0	0	1	223	0	0	1
			Surinam cherry	4	4	0	0	2	426	0	0	3
	May	1996	Surinam cherry	6	6	1	0	5	361	1	0	44
Wauchula	August	1994	Common guava	10	7	0	0	0	226	0	0	0
	January	1995	Loquat	11	11	9	0	0	639	62	0	0
	February	1995	Loquat	10	10	2	0	0	521	13	0	0
	March	1995	Loquat	10	10	4	0	0	689	32	0	0
	April	1995	Loquat	9	9	3	0	0	343	64	0	0
			Surinam cherry	2	2	1	0	0	145	37	0	0
	May	1995	Surinam cherry	3	3	3	0	1	128	92	0	11
	June	1995	Surinam cherry	6	6	3	0	1	229	58	0	1
	July	1995	Surinam cherry	2	2	0	0	0	6	0	0	0
	August	1995	Common guava	10	9	5	0	0	1185	37	0	0
	September	1995	Cattley guava	1	0	0	0	0	0	0	0	0
			Common guava	6	4	2	0	0	257	23	0	0

Site	Month	Year	Fruit sampled	Number of samples					Number of insects emerging			
				Total	With CFF[a]	With Da[b]	With Dl[c]	With Ua[d]	CFF[a]	Da[b]	Dl[c]	Ua[d]
W Palm Beach	January	1995	Loquat	1	1	0	0	0	30	0	0	0
	February	1995	Loquat	1	0	0	0	0	0	0	0	0
			Surinam cherry	4	2	0	1	0	85	0	2	0
			Common guava	1	1	0	0	0	2	0	0	0
	March	1995	Loquat	4	4	0	1	0	186	0	47	0
			Surinam cherry	2	1	0	0	1	38	0	0	5
	May	1995	Surinam cherry	2	2	0	0	0	6	0	0	0
	June	1995	Surinam cherry	2	2	0	1	0	11	0	2	0
	July	1995	Cattley guava	1	1	0	0	0	45	0	0	0
	August	1995	Cattley guava	2	2	0	0	0	12	0	0	0
			Common guava	4	3	0	0	0	24	0	0	0

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BIOGRAPHICAL SKETCH

Avraham (Avi) Eitam was born in 1960 in Toronto, Ontario, Canada, and immigrated with his family to Israel in 1969. He graduated from Hugim High School in Haifa in 1978, and served in the Israel Defense Forces from 1979 to 1982. Upon completion of military service, he enrolled in undergraduate studies at Tel Aviv University, earning his B.Sc. in Biology Magna Cum Laude in 1985. He earned his M.Sc. in Zoology, also from Tel Aviv University, in 1989. The title of his thesis was "Aspects of social behavior in two species of halictine bees."

Between 1989 and 1992, he worked in research and pest management at the Arava Research Station, Yotvata, Israel, concentrating on insect pests of the date palm. He enrolled in Ph.D. studies at the University of Florida in 1993.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John M. Sivinski, Chairman
Assistant Professor of Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Richard M. Baranowski
Professor of Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Jonathan H. Crane
Associate Professor of Horticultural Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

J. Howard Frank
Professor of Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Patrick D. Greany
Professor of Entomology and
Nematology

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May, 1998

Dean, College of Agriculture

Dean, Graduate School